



ANNALS
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NATAL MUSEUM

EDITED BY
ERNEST WARREN, D.Sc.(LOND.), DIRECTOR.



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**On the Anatomy of a New South African
Hydroid, *Bimeria rigida* sp. n.**

By

Ernest Warren, D.Sc.(Lond.).

With Plates I and II, and 2 text-figures.



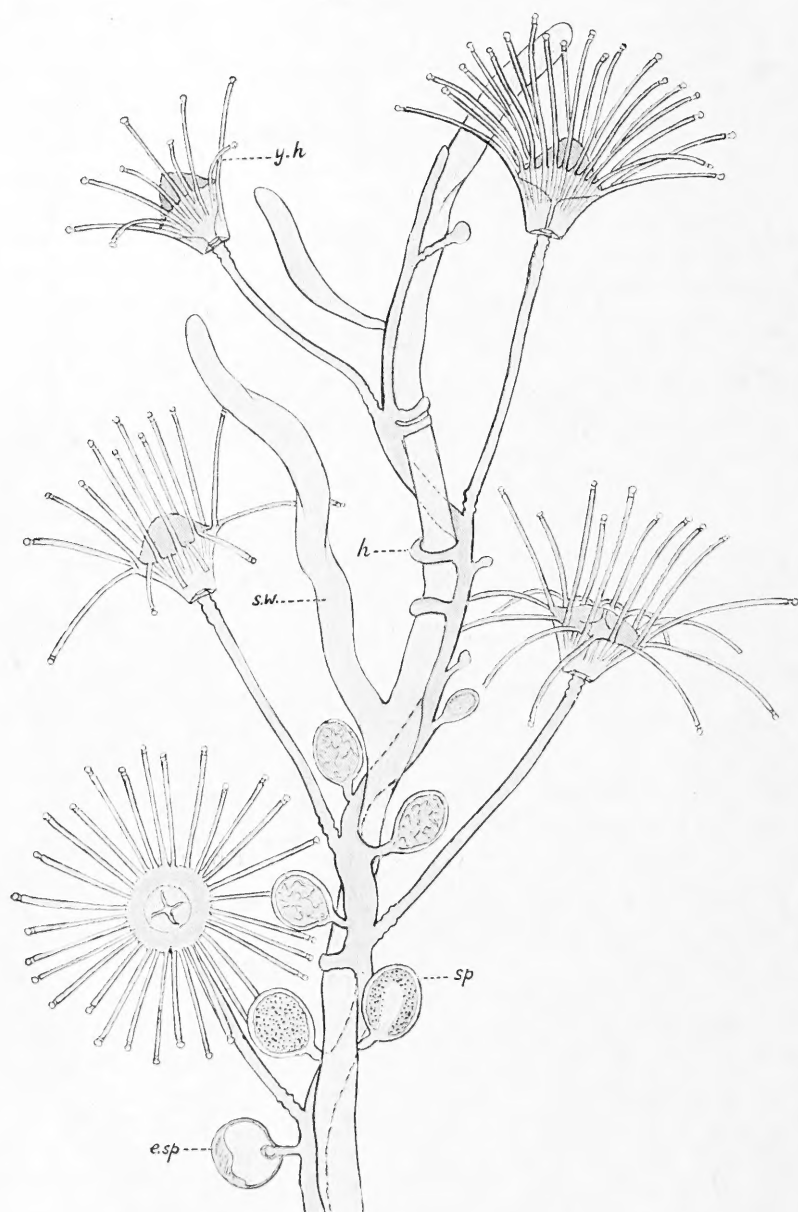
THE singular hydroid forming the subject of this paper possesses tentacles which have a somewhat limited power of movement owing to the presence of stiff perisarc which runs along their under surfaces. The specific name *rigida* has been applied to the hydroid on account of this peculiarity, which, however, is shared, but in a less developed degree, by other species of the genus, such for example as *Bimeria vestita* *Wright*.

The hydroid was found sparingly in the rock-pools at the Three Sisters Rocks, Port St. John, Pondoland, in January, 1911. The material was fixed in hot corrosive sublimate solution with 1·5 per cent acetic acid, and the sections were stained with Delafield hæmatoxylin followed by Orange.

The hydroid is small and clings to sea-weed. The hydranth, together with the pedicel, extends about 2–3 mm. beyond the weed. It is of a pale horn-colour and translucent, save for the débris and diatoms which may adhere thickly to the perisarc of the tentacles and body.

TROPHOSOME. *Hydrorhiza*.—The *hydrorhiza* creeps on the surface of delicate sea-weeds and sometimes tends to grow vertically upwards in a spiral course around narrow, upright shoots of the weed. In addition to this tendency to grow spirally, the *hydrorhiza* gives off short horizontal outgrowths

TEXT-FIG. 1.



Bimeria rigida, sp.n., growing on sea-weed; *e. sp.*, empty sporosac; *sp.*, sporosac; *h.*, clasping branch; *y. h.*, young hydranth with few tentacles; *s. w.*, sea-weed. $\times 25$.

which tightly clasp the support, recalling certain root-climbing plants (text-fig. 1). By these two means the hydrorhiza becomes very firmly attached to the smooth surface of the weed on which it is growing. The analogy to a climbing plant is further emphasised by the fact that the hydrorhiza gives off in an alternating manner hydrocaulus-outgrowths, recalling petioles, each bearing a single hydranth at the distal end. The root-like clasping organs often, although not invariably, spring from the node, or the place of origin of the hydrocaulus-outgrowth. It is interesting to note that the methods of accomplishing similar mechanical feats (namely, (1) grasping a slippery surface, (2) exposing the hydranths of the hydroid, or the leaves of the plant, to the surrounding medium in such a manner that they shall interfere with one another as little as possible) are closely alike in two totally different organisms.

The hydrorhiza is smooth and is without annulations of any kind. The diameter is about 0.095 mm. (95μ) and the thickness of the perisarc is 12–20 μ on the sides and upper surface. As usual the thickness of the perisarc is much less on the surface of attachment to the weed, and sometimes here it is almost non-existent. Very frequently the sides of the perisarc are strengthened by vertical arches or pillars some 30 μ in thickness (Pl. II, figs. 13, 14, and 15, *p.*). The structure is built for strength, and in cross-section of the hydrorhiza the perisarc resembles the span of a bridge with thick, vertical buttresses.

The outer layer of the perisarc is apparently somewhat soft and gelatinous in character, since diatoms and minute particles of mud and sand adhere to it and form a dense fringe.

Internally there is a simple cœnosarc tube of endoderm surrounded by ectoderm. There is no accessory thin ectodermal sheet lying in contact with the roof of the perisarc-tube as occurs in certain hydroids.

Hydrocaulus.—The hydrocaulus consists of branches arising from the hydrorhiza, each branch carrying a single hydranth. The branches or hydranth-pedicels do not come

off irregularly; frequently they alternate, but sometimes they appear to arise along a spiral line. The pedicel is indistinctly annulated; the ringing is more pronounced at the two ends, but especially at the proximal end. The average length of the pedicel is 2 mm. and the diameter is 80 μ . The perisarc is about 14 μ in thickness.

The coenosarc is typical except at the distal end close to the hydranth. Here the coelenteron may be absent, and we have simply an ectodermal layer with a central rod (Pl. I, fig. 8, *en.*) of modified endoderm cells with sparsely placed nuclei and no obvious cell-outlines. Sometimes the endoderm would appear to be wholly withdrawn, and there is left simply an axial rod of substance indistinguishable from mesoglea, and in cross-section the diameter may be less than that of a nucleus of an ectoderm cell.

Hydranth.—The body of the hydranth, in a moderate degree of expansion, consists of a lower region forming an inverted cone, and of a large projecting hypostome region (Pl. I, figs. 3 and 9). Between the two portions there is a ring of 16–33 tentacles.

The dimensions of a moderately distended polyp with twenty-two tentacles were: Total height .60 mm., width .40 mm.; height of hypostome region .27 mm.; depth of subtentacular region .33 mm.; average length of tentacle supported by perisarc .80 mm., and diameter of tentacle about 44 μ .

The subtentacular region of the body forms an inverted cone with a truncated apex where it joins the hydrocaulus. The perisarc of this region forms a definite calyx, and is continuous with the perisarc of the hydrocaulus. The floor of the perisarc-cup is flat or somewhat raised by a slight inpushing of the distal end of the hydrocaulus. In an adult hydranth the calyx is not wholly filled by the body, there being a well-defined empty space (figs. 3, 9, *e. cy.*) between the ectoderm and the calyx-wall. With the edge of the calyx, however, the ectoderm is in close contact. The communicating aperture between the calyx and the hydro-

caulus is quite small, but there is no inwardly projecting shelf or diaphragm.

Near the base of the calyx the perisarc is of moderate, uniform thickness. Slightly higher it is raised into ridges, and these ridges become more pronounced towards the edge of the cup, and vary in number according to the number of the tentacles. The perisarc of the ridges is apparently of firmer consistency than that between, since it stains much more intensely. The tentacles are surrounded by tubes of perisarc, and these have a greatly thickened lower wall or floor which is directly continuous with the ridge running down the calyx. This lower wall resembles the ridge in staining deeply. The upper wall of the perisarc-tube surrounding the tentacle is exceedingly thin, and is sometimes almost evanescent; it is continuous with the thick, soft, perisarc covering the hypostome region of the polyp (fig. 9, *s. pr. t.*).

The perisarc of the hypostome region is of very considerable thickness, and it completely envelopes it (fig. 3, *s. pr.*). This perisarc stains only faintly, and it has an especially roughened outer surface to which inorganic particles, diatoms, etc., become attached. It is of a soft, gelatinous nature, and does not appear to inhibit the power of contraction and expansion of the body to the extent that would be expected. It is continuous with the thin layer of perisarc forming the upper wall of the tentacle-tubes.

With regard to the soft parts of the polyp, there is a peculiarity about the mouth, which appears to be unique among the hydroids. When the polyp is in a state of rest there is a small rounded aperture at the apex of the hypostome (fig. 4, *o. e. c.*), and the soft perisarc extends to the edge of the opening. The aperture leads into a small, lenticular, ectodermal chamber with a convex floor (figs. 3 and 5, *e. c.*).

The mouth proper is a small aperture in the centre of the floor of the chamber. The mouth when slightly open appears to be four-cornered. The shape arises through the occurrence in the upper portion of the cœlenteron of four wide and greatly



projecting endodermal ridges (fig. 6, *e. pr.*). The ridges consist of two kinds of endoderm cells: (1) an inner fairly regular epithelium of columnar gland-cells, which stain deeply (fig. 10, *e. ep.*), and (2) an outer, thicker layer of vacuolated, reticular cells extending to the mesoglea (*e. v. c.*). The cells immediately bordering the inside of the mouth consist almost entirely of gland-cells (fig. 3, *g. o. e.*). Further down, the ridges begin to flatten out, and the inner gland-cells become confined to four more or less regular trefoil-shaped ridges (fig. 11) somewhat recalling the mesenteric filaments of an actinian. Below this, the cavity of the coelenteron is widened, and the inner gland-cells are spaced out (fig. 12) and do not form a distinct epithelium.

The ectoderm at the base of the body of the hydranth, where it tapers into a narrow stalk joining the coenosarc of the hydrocaulus, is thrown into folds (figs. 3, 9), and here there are numerous large nematocysts ($8.5\ \mu$ long and $3.4\ \mu$ broad). Similar nematocysts occur in the ectoderm of the hydrocaulus.

The calyx follows the movements of the hydranth to a considerable extent. This power arises from the fact that the firmer perisarc is mostly confined to longitudinal ridges, which are separated by soft, flexible perisarc. The hypostome region is covered with a thick layer of still softer perisarc which permits considerable freedom of movement.

The tentacles are capitate, and the thick perisarc on the lower surface and the thin perisarc on the upper surface extend to the margin of the capitulum (Pl. II, figs. 16, 19, 20). Running up the tentacle is an extension of the endoderm from the body of the hydranth. It is frequently quite typical, consisting of a single row of skeletal endoderm cells (fig. 17, *s. e. t.*). At times, and especially in the middle region of the tentacle, the cellular structure becomes lost, just as in the case of the coenosarc of the distal end of the hydrocaulus. The nuclei disappear, or become widely separate, and the endoderm is converted into an axial, homogeneous rod resembling mesoglea in its staining capacity (figs. 18, 20, *n. s. e. t.*).

This axial rod is nearer the upper than the under surface, so that in cross section it is very excentric in position (fig. 16, *en.*). Owing to the thinness and soft nature of the perisarc which covers the upper surface, the tentacle can bend towards the mouth. This bending would be scarcely possible if the thick, firm perisarc formed a complete tube around the tentacle. The ectoderm of the tentacle consists of peculiar, elongated, thread-like cells (figs. 18, 19, 20, *m. e. t.*) which are doubtless especially muscular in nature, and this great development of muscle is clearly correlated with the fact that considerable muscular power is required for bending the firm perisarc of the under surface.

The capitulum of the tentacle is provided in a typical manner with large, elongated nematocysts (fig. 19, *n.*). These are doubtless of use in securing prey. The similar nematocysts which occur in the ectoderm enveloped by the calyx and the perisarc of the hydrocaulus cannot be so utilised, and, if of any functional use, they can only serve to render the hydroid disagreeable in being eaten as a whole.

The food obtained by the hydranth appears to be of the usual kind; remains of small crustaceans, etc., being found in the cœlenteron. The external aperture of the apical ectoderm-chamber and the mouth proper can be very greatly extended, so that the endoderm may be widely exposed to the seawater and relatively large prey can be swallowed (Pl. I, fig 9).

The function of the ectodermal chamber is obscure. The chamber is not an accidental or occasional formation, but it is a perfectly definite structure which occurs in all the hydranths. It certainly forms a very efficient protection to the mouth, and would render it exceedingly difficult for parasites, such as pycnogonids, to enter the cœlenteron when the hydranth is at rest, or when the mouth is slightly opened for taking in water.

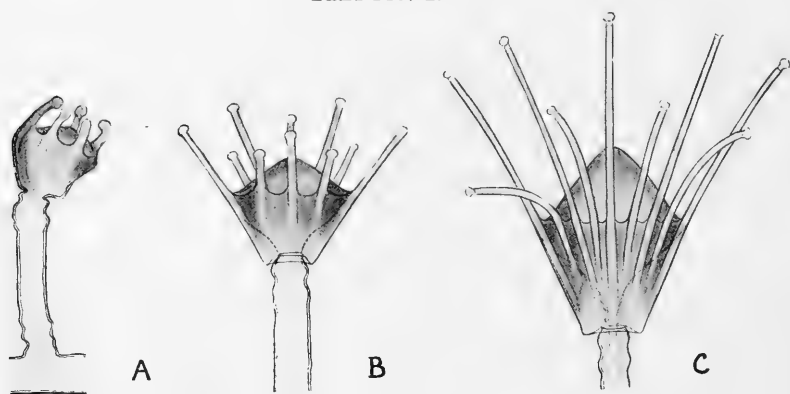
It may be noticed in this connection that the entire hydranth is singularly well protected from possible enemies by means of the great development of the perisarc. It may be further noted that we have only to suppose the ectodermal chamber



to project down into the mouth and we should have the stomodæum of the Anthozoa.

Development of the Hydranth.—The growing point of the hydrorhiza gives off outgrowths which develop into short hydrocaulus-branches bearing a single, terminal hydranth. The branch, or hydranth-pedicel, and the hydranth grow up together, the hydranth being marked out almost from the first by a slight terminal swelling to the outgrowth (text-fig. 1;

TEXT-FIG. 2.



Bimeria rigida, sp. n. A. Young hydranth with first-formed tentacles. B. Hydranth showing the formation of a second series of tentacles. C. Older hydranth with a third series of tentacles. $\times 40$.

Pl. I, fig. 1). The distal surface becomes flattened, and this will form the oral surface. There is a tendency for the columnar ectoderm cells of this flat surface to slope towards the centre even at this young stage, but the condition becomes more marked in the later stages. The whole structure, including both the young hydranth and the young pedicel, is covered by a uniform, thin and apparently soft layer of perisarc.

Around the border of the oral surface some five or six blunt outgrowths arise; these are the beginnings of the tentacles (text-fig. 2, A). They appear capitate even at this early condition. The ectoderm cells in the middle of the oral surface become deeper, and ultimately a horizontal split

is formed in them, and this is the beginning of the ectoderm-chamber (Pl. I, fig. 2, *e. c.*). The whole hydranth is still uniformly covered with perisarc, but that forming the lateral walls begins to thicken and will ultimately form the cup or calyx. The ectoderm of the polyp is in close contact with the calyx-wall at this stage.

The tentacles elongate and the cuticle or perisarc over the capitula becomes evanescent. On the calyx some trace of longitudinal ridges continuous with the tentacles can now be observed (text-fig. 2, A). The young hydranth grows, and a second series of tentacles arises alternating with the first series, and additional longitudinal ridges on the calyx-wall originate between those which are already present (B). When the tentacles of the second set have grown considerably a third series is produced (C).

In a cross-section through the calyx, smaller ridges alternating with larger ones may be noticed; the former belong to the last-formed tentacles (Pl. I, fig. 7, *r. y. t.*). The older, larger tentacles are sometimes held more upright than the younger, shorter ones which may tend towards the horizontal position. Thus the tentacles of the hydranth may be alternately raised and depressed, a common feature in many hydroids (text-fig. 1, *y. h.*).

The subtentacular region of the body gradually contracts from the calyx, leaving a space which increases as the polyp grows older (figs. 7 and 9, *e. cy.*). A mouth is formed between the ectoderm-chamber and the coelenteron, and the chamber communicates with the exterior by a central aperture.

The perisarc now thickens until the adult condition is attained.

As the polyp grows older the lumen in the distal coenosarc of the hydrocaulus becomes constricted (fig. 8), and sometimes nothing but mesoglea may remain.

GONOSOME.—The reproductive bodies are in the form of fixed gonophores surrounded by a firm layer of perisarc. Only the male gonophore has been discovered. The gonophores are oval or rounded in outline, and they are carried

directly by the hydrorhiza on short pedicels of about .08 mm. in length (text-fig. 1, *sp.*). The pedicels are not distinctly annulated. The dimensions of the gonophores vary considerably; the measurements of three were: .45 × .30; .35 × .24; .31 mm. × .18 mm.

The gonophore represents a medusa, but no umbrella-cavity is formed during development, and in the adult gonophore there is only a single layer of ectoderm, instead of a layer covering the spadix and a layer lining the inside of the perisarc, as would occur in the case of a more highly-developed gonophore.

The spadix in the adult gonophore has endoderm branches springing from it, which run through the spermatie tissue towards the periphery (Pl. II, figs. 25, 26); these endoderm branches are met by a small cluster of elongated ectoderm cells (*c. ec.*) which are continuous with, and form part of, the ectoderm lying just within the perisarc layer.

In the youngest gonophores no genital cells are observable (Pl. II, fig. 21). When slightly older scattered genital cells (fig. 22, *g.*) in the ectoderm can be noticed. These cells have not been seen to migrate from the endoderm of the hydrocaulus or hydrorhiza, and apparently they arise in situ. The genital cells become concentrated in clumps (fig. 23) and active proliferation takes place, forming compact masses of spermatocytes separating the ectoderm from the endoderm of the spadix (fig. 24). The gonophore continues to grow as a whole, and the endoderm remains adhering to the ectoderm at certain places, and there the endoderm becomes drawn out into diverticula (figs. 24 and 25, *e. d.*) which are connected with the ectoderm layer by the elongated cells (*c. ec.*) above mentioned. Ultimately growth ceases and the spermatocytes undergo the last division into spermatozoa (fig. 27, *spz.*), and soon clumps of ripe spermatozoa with tails (*r. sp.*) can be seen. During the proliferation of the spermatocytes the endoderm cells of the spadix increase in size and project into the cœlenteron in a swollen condition, and the nuclei become enlarged (cf. figs. 24 and 25).

When the spermatozoa are ripe the distal portion of the perisarc-envelope gelatinises, and the spermatozoa appear to pass through this softened swollen portion (fig. 28, *sw. pr.*) without any definite rupture occurring. It has been noticed that the ectoderm of the gonophore forms a conspicuous columnar epithelium at the distal end (figs. 24 and 25, *d. p.*), forming a kind of covering-cap or "Deckenplatte" immediately under the perisarc which becomes softened. It is suggested that this epithelium produces a secretion which causes the perisarc to swell and soften at the distal portion which thus subserves the function of the operculum so commonly met with in the gonotheca of the Calyptoblastica.

SYSTEMATIC POSITION.—The only species of *Bimeria* which are traceable in the available literature are the following: *Bimeria vestita* Wright, British Isles; *Bimeria gracilis* Clark, San Diego, California; *Bimeria robusta* Torrey, San Pedro, California; *Bimeria franciscana* Torrey, San Francisco Bay; and *Bimeria annulata* (Nutting), Santa Catalina Islands, California. Judging from the descriptions, a branching hydrocaulus is present in all the above species, but in *B. rigida* the hydrocaulus consists simply of the hydranth-pedicels which spring directly from a slightly branched hydrorhiza. The amount of extension of the perisarc over the hydranth is variously described in the different species; but clear figures are not given except in the case of *B. vestita*, where Allman shows the perisarc extending around the proximal two-thirds of the hypostome region. In none of the species are the tentacles capitate as in *rigida*.

The production of gonophores directly on the hydrorhiza is only found in the new species.

The peculiar characters of the present species are:

- (1) The simple nature of the hydrocaulus.
- (2) The great development of perisarc over the hydranth; it extends almost to the edge of the capitula of the elongated tentacles, and over the whole of the hypostome region.

(3) The presence of a small ectoderm-chamber above the mouth: morphologically, this is almost of the nature of a stomodæum.

(4) The tentacles terminate in small, but perfectly distinct, capitula, with well-developed nematocysts.

These differences are undoubtedly considerable, but unfortunately there is no general criterion for determining the amount of difference allowable between the species of a genus, and it has been thought unnecessary at the present time to separate the species *rigida* from the genus *Bimeria*.

The genera *Wrightia*, *Parawrightia*, *Garveia*, and *Bimeria* are undoubtedly related to one another. In all these genera there is a formation of a definite perisarc-cup around the hydranth, and the gonophore is in the form of a sporosac surrounded by a firm layer of perisarc.

Since the above was written Dr. James Ritchie, of the Royal Scottish Museum, has very kindly sent to me notes on certain allied hydroids which are described in journals unobtainable in this country. He writes: "The species which seems to me to come nearest to yours in habit is *Garveia grœnlandica* *Levinson*. It bears branched creeping hydrorhiza, from which simple polyps project. . . . *Bimeria corynopsis* *Vanhoffen*, from Gauss Station, in the Antarctic, has 4-5 polyps on a stem, and your specimens bear no resemblance to this species."

By placing the present species in the genus *Bimeria*, Dr. Ritchie points out that no weight is given to the character of the capitulation of the tentacles, and, judging from a rough sketch sent to him, he suggests that possibly the present species may really fall into Pictet's genus *Sphærocoryne*. The habit of growth of *Sphærocoryne bedoti* *Pictet*, from Ambouia, is very similar to that of *B. rigida*, the tentacles are capitate, and the shape of the hydranth is also much the same. *S. bedoti* differs, however, in (1) the perisarc stopping at the base of the hydranth, (2) the tentacles being arranged in several compressed verticils, and (3) it is believed that free-swimming medusæ are formed, and these

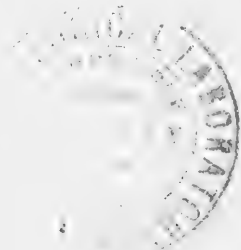
arise from the body of the hydranth in the neighbourhood of the tentacles.

With these marked dissimilarities I am reluctant to refer *rigida* to the genus *Sphærocoryne*. The capitula of *rigida* are small although perfectly definite structures, and it is easier to suppose that their production is associated with the enclosure of the tentacles with the perisarc rather than that it indicates a coryne-like ancestor. A character such as the capitation of tentacles could, we may readily suppose, easily originate independently several times in the hydroid series.

As far as can be judged from the published descriptions of the species of *Bimeria*, the perisarc-cup is closely adherent to the ectoderm of the hydranth, but such is not the case in *B. rigida*, for in the proximal region the body of the hydranth is widely separated from it (Pl. I, figs. 3, 9).

The true calyx of the *Calyptoblastica* differs from the perisarc-cup of the *Gymnoblastica* in that typically in the former the body of the adult hydranth is free from the mouth of the calyx. The calyx is, as a rule, relatively large, and the hydranth can retract into it. In some *Calyptoblastica*, however, as in *Sertularella spp.*, *Sertularia spp.*, and *Thyroscyphus spp.*, the calyx is lined by a layer of ectoderm, which near the mouth-edge of the calyx may bear a well-developed battery of nematocysts. The calyx is secreted by the ectoderm of the hydranth-bud, and then, subsequently, this ectoderm splits into an inner and outer layer. The inner layer forms the ectoderm of the body of the hydranth, and the outer layer, which consists of a thin sheet of flat cells, forms a lining to the calyx. The lining ectoderm layer is by no means always present in the adult calyx, as, for example, in *Plumularia*; but whether this absence is due to the non-occurrence of the splitting of the ectoderm of the hydranth-bud, or to the subsequent disappearance of the outer layer, has still to be determined.

A quite similar splitting of the ectoderm occurs in the case of the gonangia of the *Calyptoblastica*. The ectoderm of



the gonangium-bud secretes the perisarc of the gonotheca and afterwards splits, except in the region of the "Deckenplatte," into an outer layer which lines the gonotheca and an inner layer which covers the blastostyle.

In the Calyptoblastica these accessory sheets of ectoderm may be present on the "dorsal" or abcauline surface of the coenosarc of the hydrocaulus, and also around the hydranth and gonangium. The layers are closely adherent to the perisarc, and they must certainly serve to anchor the living tissues to the supporting structure, and possibly this is the main function. Quite likely the cells may be especially contractile, and the so-called opercular muscles of the hydranth appear to be portions of this sheet. I have had no opportunity of observing whether these reputed muscles actually serve to move the opercular flaps. In this connection it may be mentioned that the lining sheet of ectoderm is well developed around the hydranth of *Sertularia acanthostoma Bale*, although there are no opercular flaps and the margin of the calyx is dentate.

These accessory sheets of ectoderm have not been found in the coenosarc of any of the Gymnoblastica that I have examined, and their formation would seem to be a somewhat characteristic feature of the Calyptoblastica. Their non-occurrence in *Bimeria rigida* serves to indicate that this species, notwithstanding the presence of a kind of calyx, is not necessarily to be regarded as a step in the direction of the calyptoblastic hydroids.

In *Bimeria rigida* practically the whole of the hydranth is invested by a thick layer of perisarc, and this is closely adherent to the ectoderm except at the base of the polyp.

With respect to the perisarc it is very doubtful if *Bimeria rigida* is to be regarded as especially intermediate between the Gymnoblastica and Calyptoblastica. The calyptoblastic condition probably arose from such a stage as is exhibited by *Coryne virgata Allman*, where the hydranth-bud is conspicuously enclosed by perisarc, and this perisarc persists to an appreciable degree around the body of

the adult hydranth. A similar envelope persisting around a modified person producing a cluster of gonophores, such as the blastostyle of *Heterocordyle*, would clearly give rise to the gonotheca of the *Calyptriblastica*.

In *Bimeria rigida* it is quite certain that the sporosac is a reduced medusa and not a blastostyle producing one gonophore, for in the related *Parawrightia* well-formed radial-canals are present in the structure. Thus, notwithstanding the development of a calyx, *Bimeria rigida* must be regarded as a true gymnoblastic hydroid. The development of perisarc is a means of defence, and in this species we reach what would appear to be the maximum development possible in the *Gymnoblastica*.

From such a condition as is seen in *Coryne virgata* we pass on the one hand to *Bimeria rigida* of the *Gymnoblastica* and on the other hand to the operculate forms of the *Calyptriblastica*.

It can be readily understood that a thick layer of perisarc closely investing the body of the hydranth is bound to inhibit movement to some extent, and to prevent a rapid response to an external stimulus notwithstanding the occurrence of especially flexible perisarc on the hypostome region and on the oral face of the tentacles. In the case of the *Calyptriblastica* the hydranth when extended from the cup has the advantage of perfect freedom of movement, while rapid withdrawal into the calyx provides a very efficient protection against enemies.

Finally, it may be said that in *B. rigida* we reach the extreme type of protection by perisarc production in the *Gymnoblastica*, and this apparently has not proved a great success, since the condition is rare or almost unique. The formation of a true calyx free from the body of the hydranth and into which the hydranth can be withdrawn and enclosed by opercular folds, or protected by overhanging teeth, has clearly proved a more effective method of protection, since calyx-bearing hydroids are the dominant forms of the present day.



EXPLANATION OF PLATES I AND II,

Illustrating Dr. Ernest Warren's paper, "On the Anatomy of a New South African Hydroid, *Bimeria rigida* *sp. n.*"

FIG. 1.— $\times 180$. Vertical, longitudinal section of young hydranth before the tentacles have appeared; covered with a thin, continuous layer of perisarc.

FIG. 2.— $\times 180$. Vertical, longitudinal section of young hydranth with tentacles in process of growth; mouth has not yet been formed; covered with a thin, continuous layer of perisarc. In the middle of the hypostome region the ectoderm has thickened, and a split (*e. c.*) has appeared in it; this is the beginning of the ectoderm cavity which is formed above the mouth.

FIG. 3.— $\times 180$. Vertical, longitudinal section of an adult hydranth, showing soft perisarc (*s. pr.*) over the hypostome region and extending over the upper surface of the tentacle, ectoderm chamber (*e. c.*), glandular oral endoderm (*g. o. e.*), two of the four endoderm projections (*e. pr.*), empty calyx-cavity (*e. cy.*) and nematocysts (*n.*).

FIG. 4.— $\times 180$. Transverse section near apex of hypostome of adult hydranth, showing soft perisarc and opening of ectoderm chamber (*o. e. c.*) to the exterior.

FIG. 5.— $\times 180$. Transverse section of hypostome region at the level of the mouth, showing ectoderm chamber (*e. c.*) and mouth (*m.*).

FIG. 6.— $\times 180$. Transverse section of hypostome region at some little distance below the mouth, showing the four endoderm projections (*e. pr.*).

FIG. 7.— $\times 180$. Transverse section through calyx region, showing empty cavity (*e. cy.*), calyx-wall with perisarc ridges of older tentacles (*r. o. t.*) and of younger tentacles (*r. y. t.*), and the lower portion of the body of the hydranth with coelenteron (*Cæ.*).

FIG. 8.— $\times 180$. Transverse section through the hydrocaulus just below the hydranth, showing the solid endoderm (*eu.*) with coelenteron entirely occluded.

FIG. 9.— $\times 180$. Vertical, longitudinal section of expanded adult hydranth in feeding attitude, showing endoderm projections (*e. pr.*), the glandular oral endoderm (*g. o. e.*) exposed to the water, the ectoderm chamber (*e. c.*) thrust to the edge, and the muscular ectoderm (*m. e. t.*) of the tentacle.

FIG. 10.— $\times 300$. Horizontal section of an endoderm projection close

to the mouth, showing a well-marked inner epithelium (*e. ep.*) covering a mass of vacuolated endoderm cells (*e. v. c.*)

FIG. 11.— $\times 300$. Horizontal section of endoderm of hydranth immediately below the endoderm projections (*e. pr.*). There is a tendency for the formation of a definite inner epithelium of gland-cells on four trefoil-shaped endoderm ridges.

FIG. 12.— $\times 300$. Horizontal section of endoderm near base of hydranth in which the cells are mostly vacuolated; gland-cells (*e. ep.*) are few, and scattered at the periphery.

FIG. 13.— $\times 300$. Transverse section of hydrorhiza, showing the thin perisarc floor (*f.*) in contact with sea-weed (*s. w.*) and a vertical, supporting pillar (*p.*).

FIG. 14.— $\times 300$. View from above of a piece of hydrorhiza, showing vertical pillars (*p.*) on each side.

FIG. 15.— $\times 300$. Internal view of piece of hydrorhiza with one side removed, showing three vertical pillars (*p.*), thin floor (*f.*), and thick roof (*r.*).

FIG. 16.— $\times 600$. Tentacle of hydranth in transverse section, showing soft upper perisarc (*s. pr. t.*), endoderm axis (*eu.*), especially muscular ectoderm (*m. e. t.*) and thick, firm, lower perisarc (*f. pr.*).

FIG. 17.— $\times 600$. Piece of tentacle in longitudinal, vertical section, showing septate endoderm axis (*s. e. t.*).

FIG. 18.— $\times 600$. Piece of tentacle in longitudinal, vertical section, showing non-septate endoderm axis (*n. s. e. t.*); diatoms and other débris (*d.*) are attached to the lower, thick, firm perisarc.

FIG. 19.— $\times 600$. Distal end of tentacle in horizontal section, showing nematocysts (*n.*) in the naked capitulum.

FIG. 20.— $\times 300$. Horizontal section through whole length of tentacle, showing its origin from the hydranth and the perisarc covering.

FIG. 21.— $\times 180$. Section of young gonophore being budded from hydrorhiza.

FIG. 22.— $\times 180$. Section of a somewhat older gonophore, showing the first sign of genital cells (*g.*).

FIG. 23.— $\times 300$. Section of a small piece of the gonophore, showing a group of genital cells (*g.*) in the ectoderm.

FIG. 24.— $\times 180$. An older gonophore in vertical, median section, showing the beginning of the endoderm diverticula (*e. d.*) and the ectoderm cap-cells (*d. p.*) resembling the "Deckenplatte" of the Calyptoblastica.

FIG. 25.— $\times 180$. Vertical, median section of adult gonophore, with endoderm diverticula (*e. d.*) meeting clumps of elongated ectoderm cells

(*c. e. c.*) which form a portion of the ectoderm epithelium lining the gonophore.

FIG. 26.— $\times 180$. Transverse section of gonophore, showing spadix (*sp.*) and the mass of spermatoocytes (*spcy.*).

FIG. 27.— $\times 180$. Vertical tangential section of gonophore, showing endoderm diverticula in transverse section (*e. d.*), the thin ectoderm epithelium (*ec. ep.*), the mass of spermatozoa (*spz.*), and the clusters of ripe spermatozoa (*r. sp.*) in which tails have been formed.

FIG. 28.— $\times 180$. Empty gonophore-case; the spermatozoa have been discharged through the gelatinised upper portion (*sw. pr.*). The swelling up of this portion of the perisarc apparently arises through the action of the ectoderm cap-cells (*cf. d. p.*, figs. 24, 25).

EXPLANATORY REFERENCES.

c. ec. Elongated connecting ectoderm cells between ectoderm lining the sporosac and endodermal diverticulum. *Cæ.* Cœlenteron.

d. Diatoms and other débris. *d. p.* "Deckenplatte" or ectodermal cap-cells.

c. c. Ectodermal chamber. *e. cy.* Empty calyx-cavity. *e. d.* Endodermal diverticulum. *e. ep.* Endodermal epithelium lining cœlenteron. *c. pr.* Endodermal projection. *e. sp.* Empty sporosac. *e. v. c.* Endodermal vacuolated cells. *ec. sp.* Ectoderm lining sporosac. *en.* Endoderm.

f. Thin floor of perisarc of hydrorhiza. *f. pr.* Firm perisarc.

g. Genital cells in ectoderm of sporosac. *g. o. e.* Glandular oral endoderm.

m. Mouth. *m. e. t.* Muscular ectoderm of tentacle.

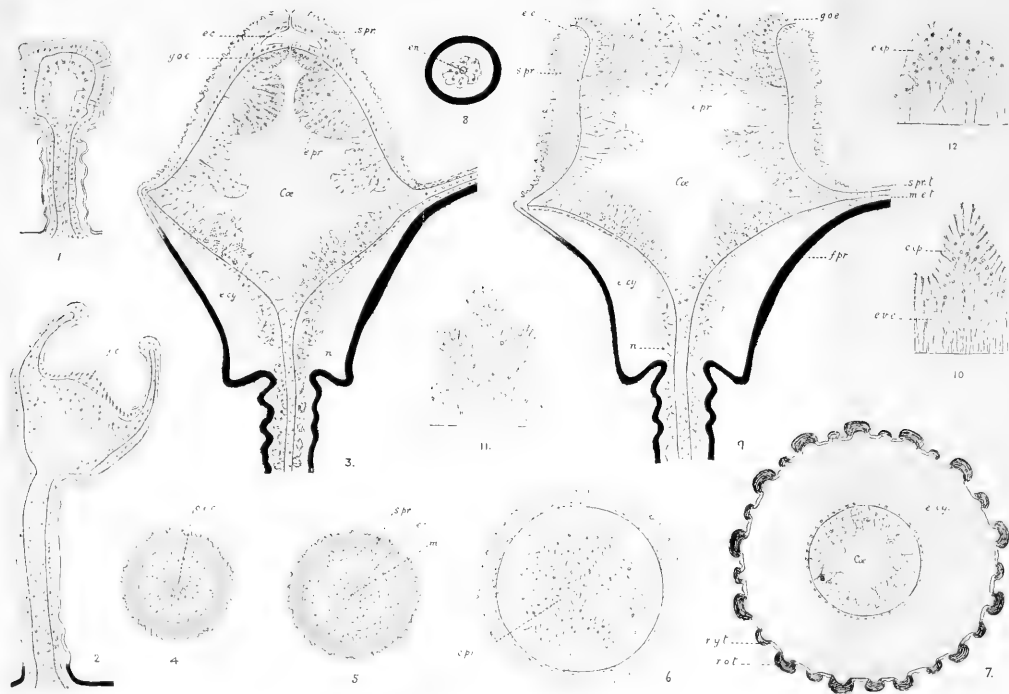
n. Nematocyst. *n. s. e. t.* Non-septate endodermal axis of tentacle.

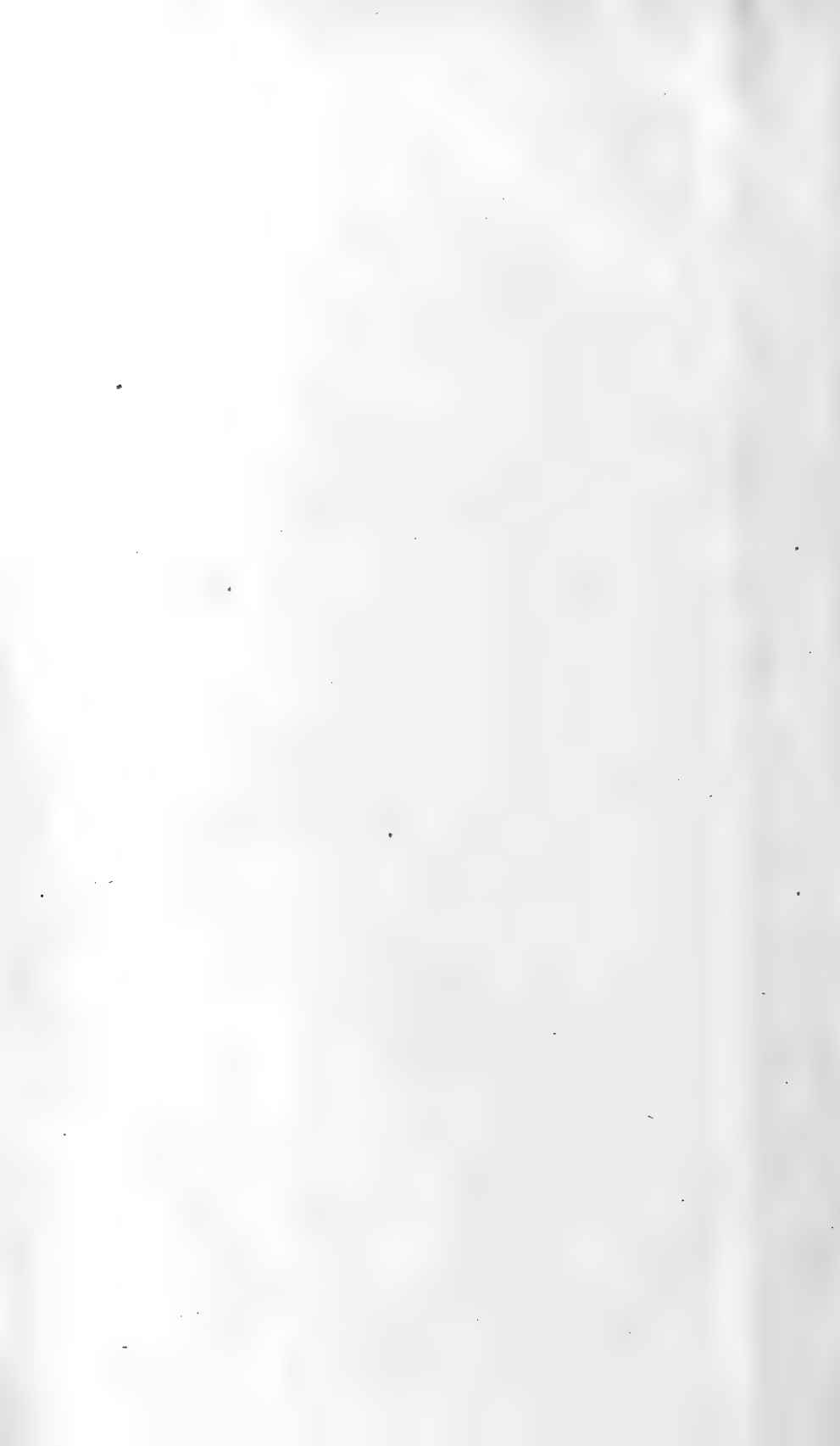
o. e. c. Opening of ectodermal chamber to exterior.

p. Supporting vertical pillar of perisarc in hydrorhiza.

r. Perisarc roof of hydrorhiza. *r. o. t.* Ridge of older tentacle on calyx. *r. sp.* Clump of ripe spermatozoa with tails. *r. y. t.* Ridge of younger tentacle on calyx.

s. e. t. Septate endoderm of tentacle. *s. pr.* Soft perisarc. *s. pr. t.* Soft perisarc on upper surface of tentacle. *s. w.* Sea-weed. *sp.* Spadix of gonophore. *spcy.* Spermatoocytes. *sw. pr.* Swollen perisarc. *spz.* Spermatozoa.







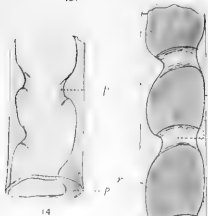
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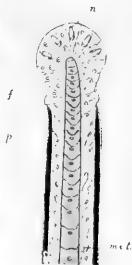
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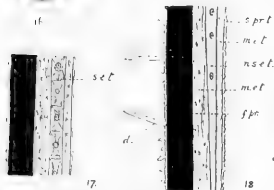
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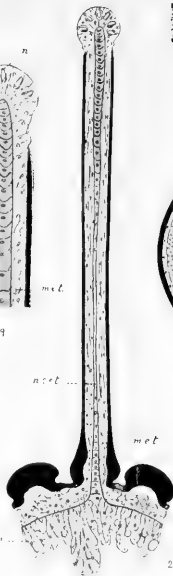
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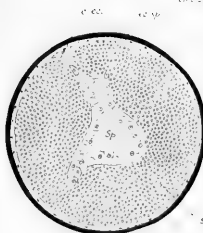
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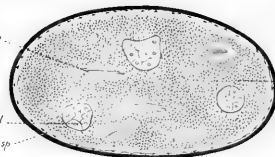
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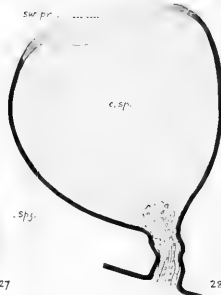
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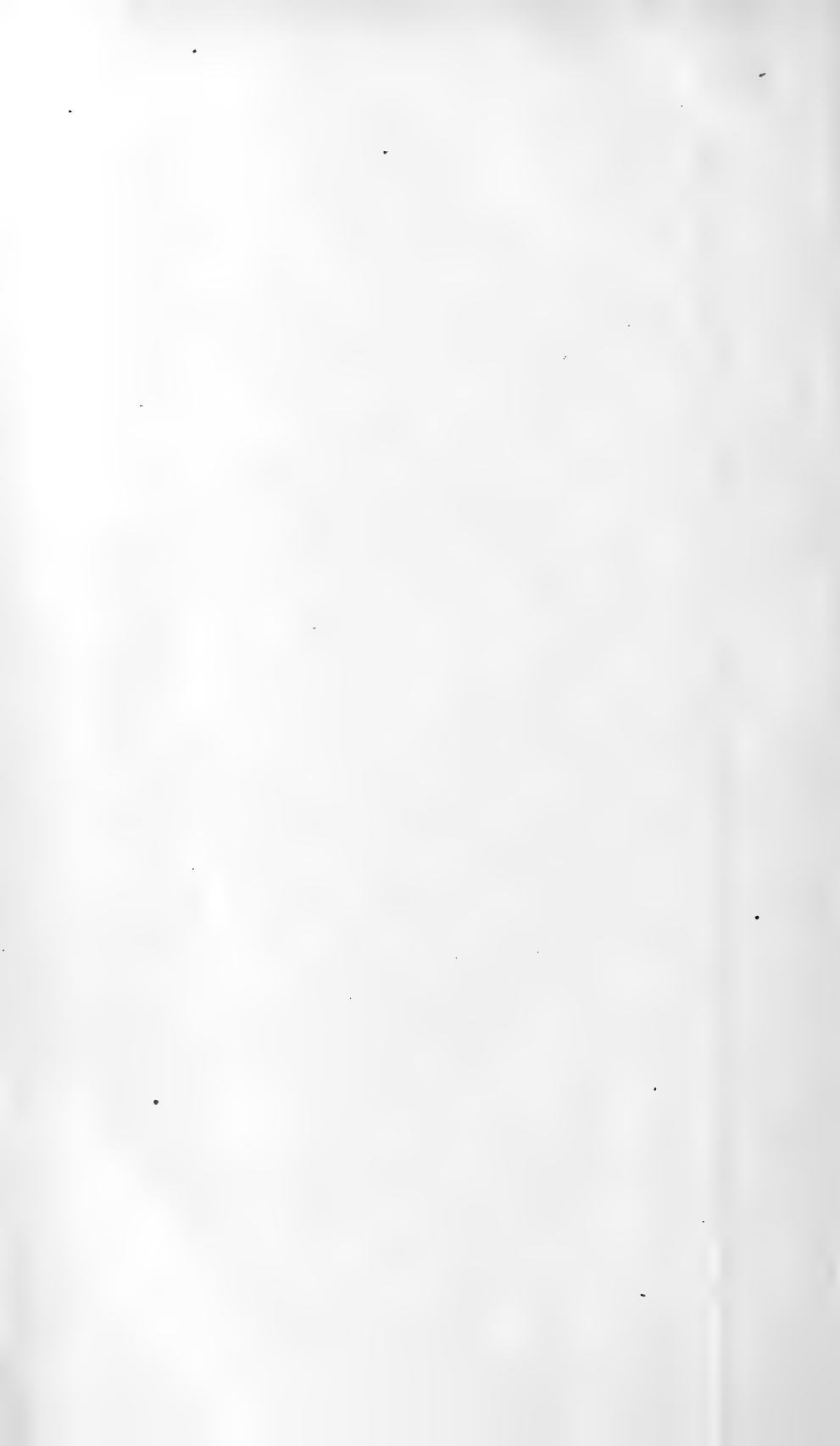
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24.



28.



The Wing Venation and Respiratory System of Certain South African Termites.

By

Claude Fuller,

Division of Entomology, Department of Agriculture, Pretoria.

With Plates III—XI.

(Read at a Meeting of the South African Biological Society, Pretoria,
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REVIEW.

CERTAIN results of this investigation appear to be at variance with usually accepted views on wing-venation, and for the sake of clearness the main features of the present paper are briefly summarised in the following paragraphs :

(1) The series of ribs supporting the termite wings are derived from thickenings of the cellular tissue of the developing organ.

(2) One of these thickenings is in the form of an ambient, and develops independently around the margin, whilst the rest form about tracheæ. Subsequently, that portion of the ambient thickening which extends along the outer margin is converted into the rib costa.

(3) The ontogeny of the tracheæ in a termite wing-sac does not support the generalised scheme of Comstock and Needham, in which all the tracheæ spring from an anterior and posterior trachea arising respectively from the dorsal and ventral longitudinal tracheæ of the thorax.

(4) The tracheæ of the wing-sac develop from two or from three buds forming very early in nymphal life upon each of the four sections of the spiracular trunk tracheæ within the meso- and metathorax and not upon the dorsal and ventral longitudinal trunks.

(5) The position and branching of the longitudinal ribs of the wing are almost wholly dependent upon the position and

development of the longitudinal tracheæ, except in the case of the costa, which is not preceded by a trachea. That the costa is not preceded by a trachea is confirmatory of the views of Fritz Müller, Spüler, Brauer, and Redtenbacher.

(6) From the examination of *Calotermes durbanensis* Hav., the fundamental or primitive scheme would appear to be for the ribs, Radius, Media, and Cubitus to be associated with the main wing-sac tracheæ which arise separately from one another from the spiracular trunk tracheæ of the thorax.

(7) The variation in the venation, so decidedly characteristic of the termite wing, is chiefly due to the erratic development of the tracheæ of the wing-sac.

(8) The extra principal ribs frequently met with in a termite wing are due to the growth of extra principal tracheæ in the wing-sac.

(9) The specialisation of the wing-ribs, apart from the costa, is one of reduction; first, in the degree of branching, and then in complete atrophy. This is dependent upon a more or less equal reduction in the tracheæ of the wing-sac.

(10) The respiratory system of a newly-hatched termite consists of a framework of comparatively few simple tracheæ, from which a multitude of dichotomising, arborescent, and other tracheæ gradually develop and grow.

(11) The specialisation of the respiratory system is one of reduction, the nascent system of the more specialised termites (Metatermitidæ) being less extensive than is that of the more generalised termites (Protermitidæ and Mesotermitidæ). The principal difference is the presence of a pair of ventral longitudinal trunk tracheæ in the Pro- and Mesotermitidæ and the absence of such in the Metatermitidæ.

(12) The valvular spiracles of the abdomen of an adult termite are derived by gradual transformation from the occluding apparatus of the spiracles with a fixed opening exhibited by the nymphs; and this transformation is more decided in the females than in the males.

(13) The slit-like spiracles of the abdomen of highly distended females (queens) of the Holmgren genera *Termes* and

Odontotermes represent disruptions of the final valvular spiracles.

I. INTRODUCTION.

This contribution towards a knowledge of certain Termite features rests upon a number of limited studies of various local species that I have been able to make from time to time. Each study is at best imperfect, because I have been limited by want of opportunity and material; and, further, because the phases of structure and development recorded have been investigated by ready and simple methods of examination. For this latter reason the anatomical details are separated by many lacunæ, gaps that might have been filled at the time had the technique employed been more elaborate. It was not, however, my original intention to pursue the matter as far as I have. With a view to establishing a satisfactory working nomenclature for the ribs of the termite wing, I first turned for guidance to the tracheation of the developing organ, and this led me to examine the general respiratory system. That wing-venation and the tracheal system can be treated together shows how inseparably the two are connected.

As a result, certain independent conclusions had been arrived at, and a radical change made in the accepted nomenclature of the wing-ribs. It is possible that these may bring me into conflict with what is regarded by a large school of modern entomologists as the last word upon the subject; in any case, they invite criticism. Should such criticism lead to a more thorough examination of the termite wing and its ontogeny by others more competent to handle the subject, my efforts will have served a good purpose even if it be shown that, in company with many another isolated observer, I have made some fundamental errors.

It will have been noticed that the supports of the wing are spoken of as ribs, not as "veins" nor as "nervures." On the other hand, the assemblage of these ribs is called

venation. The use of either "vein" or "nervure" implies an adherence to one or another school of entomology; from this objection the more homely rib is free. But, in referring to the several supports of the wing as ribs, one should perhaps apply costation to the assemblage. It would be capricious, however, to introduce a new term when venation is so generally employed.

Upon the whole, few new terms have been introduced, and then only to meet special cases or to avoid prolixity. Generally, terms will be found employed in the broad sense of their common acceptance by entomologists or botanists.

The generic and family names used are those of Holmgren's classification.¹ Unfortunately, the specific name of a termite under reference cannot always be indicated; such is referred to the genus or subgenus into which it falls in the classification mentioned. This, together with a desire to avoid a too frequent repetition of the names of recognised species, leads to certain characteristics being described as generic. In every case, however, it is to be understood that any such statement does not involve the genus further than those South African species enumerated in the Appendix.

Sometimes the word "wing" is applied to the developing organ, but, ordinarily, this is spoken of as the "wing-sac."

Except for those that are obviously diagrammatic, the illustrations reproduce some of my many camera-lucida sketches, as faithfully as possible, with a none too facile pen.

It is to be noted, however, that in most cases when the wing-sac of a more or less mature nymph is treated, the basal connections of the principal tracheæ are simplified. In such wing-sacs, after entering the shoulder and thoracic cavity, these tracheæ are profoundly looped; often more so than in figs. 140 and 153 (Pls. IX, X). To reproduce them as they are actually arranged would give a very involved illustration. The loops are, therefore, eliminated and the basal connections shown as they appear in young nymphs.

¹ Holmgren, Nils, 'Termitenstudien,' parts i, ii, iii; Upsala and Stockholm, 1909, 1911, 1912.

Further, in mature nymphs the median trachea is in contact with either the radial or the cubital in the base of the wing-sac; in the figures it is shown separated.

II. THE ORIGIN OF WING-VENATION.

The wings of termites seem to be the final form of pouch-like expansions of the meso- and metathorax. Tracheæ are not absent from "the wing fundamentals" as has been stated, and the buds, from which later on they develop, certainly form before any thoracic extension is noticeable.

In 1906 Woodworth¹ developed a general theory of wing-venation which suffered criticism because he ignored, or set out to controvert, the accumulated evidence showing the venation of the insect-wing to be derived from the tracheation of the developing organ, or, as he rather sceptically puts it: "The veins simply represent the tracheal arrangement." He argued: "The more rational conception is that there existed at the beginning and has existed through all time to the present day, a mechanical necessity, in accordance with which the primitive venation was produced and all its essential features have been maintained through all the vicissitudes of the ages . . . mechanical necessities are the dominant factor in their (the veins) first production and in their subsequent development." This theory may be said to apply to the ontogeny of wing-ribs described by Lowne,² as follows: "The walls of the wing-sac become plicated in fan-like folds, radiating from its attachment to the thorax, the angles of the folds become thickened and form the primary veins."

Whilst the elaboration of Woodworth's theory finds no place here, his suggestion of a marginal vein is important. He says little more than this: "One of the first veins to appear is the marginal. . . . The marginal vein is often not uniform in size around the whole wing, being usually strongest on the front margin, often weak on the hind margin,

¹ Woodworth, C. W., "The Wing Veins of Insects," University of California, Technical Bulletins, vol. i, pt. i, 1906.

² Lowne, B. T., "The Blow Fly," London, 1890-5.

and quite commonly entirely absent on the outer (distal) edge of the wing." What else is said has but to do with an imagined ontogeny. The point is that the termite wing does possess a marginal rib, which is pronounced along the outer margin and often more or less faded out along the inner; it is, in no conceivable manner, derivable from an immediate or remote tracheal forerunner.

Among earlier writers, Fritz Müller, Spüler, Brauer, and Redtenbacher claimed that the wing-ribs arose from pre-existing tracheæ except, they held, that the outermost or costa did not have a trachea as its origin and therefore had nothing to do with the "veins." Comstock and Needham,¹ in a very able and convincing demonstration, seemingly succeeded in showing that all the ribs, including the costa, were in the beginning preceded by tracheæ; unfortunately, they give no particulars of their studies of the wing tracheæ of Termites, otherwise I might have found no difficulty in reconciling myself to their view. Their studies enabled them to make the following definite announcement: "It can be accepted as a firmly-established fact that the courses of the wing-veins of primitive insects were determined by the courses of the pre-existing tracheæ." So far as termite wings are concerned, the studies now submitted will show that those ribs that are preceded by tracheæ reflect the courses and developments of those tracheæ; and, the more generalised the wings, the more is the individuality of a pre-existing trachea recorded in the final wing. The studies, however, controvert the doctrine that the costa is also preceded by a trachea.

As one of the main features of their thesis, these authors put forward "a hypothetical type to which the wings of all orders might be referred." They indicated the primitive condition of the basal connections of the wing-tracheæ and devised two routes of specialisation, one of addition, the other of reduction.

The hypothetical type was "represented by the tracheæ

¹ Comstock, J. H., and Needham, J. G., "The Wings of Insects," 'The American Naturalist,' vols. xxxii, xxxiii.

which precede the forming veins," and accorded well with the venation of the most generalised wings they presented. All the principal veins are traced to two tracheæ which enter the wing-sac, one on its anterior and one on its posterior border. The anterior is described as "a branch of the dorsal longitudinal trachea," the posterior, "of the ventral longitudinal trachea." Unfortunately, these two tracheæ are not further defined. Such tracheæ are present in our more generalised termites (*Hodotermes*, *Calotermes*, *Cryptotermes*, and *Rhinotermes*), but the basal connections of the wing tracheæ are far removed from them. According to the type, each of the two wing tracheæ, on entering the wing-sac, subdivided into four principal stems so as to form an anterior and a posterior group. The anterior shows the costal, the sub-costal, and the radial as outer branches of the medial trachea; the posterior shows three anals as inner branches of the cubital trachea. To each principal trachea was given a typical development, some being simple and others variously branched (fig. 1, Pl. III).

As reflected in the figure, the type was enlarged as follows: "In most insects there has been developed a transverse trachea connecting these two groups of tracheæ. . . . Frequently the transverse basal trachea is indistinguishable from the two main trunks which it connects, the three forming a single, continuous transverse trachea from which arise all the wing tracheæ. . . . When a basal trachea is formed the medial trachea tends to migrate along it towards the cubito-anal group and often becomes united with that group. In some cases the base of the radial trachea tends to follow the base of the medial in its migration along the basal trachea towards the cubito-anal group." This linking up of the two groups of tracheæ (as shown by the dotted lines in the figure) is regarded by the authors as a more specialised condition. Inasmuch as the principal tracheal stems within the wing-sacs of all the termites I have examined are post-embryonic developments from the spiracular trunks¹ and not from the

¹ See Section V for definition of "spiracular trunk," etc.

dorsal or ventral longitudinals; and almost invariably issue from these trunks between the arms of the Y-shaped tracheæ of the second and third legs, fig. 48 (Pl. V), there would appear to be little relation between the termite system and that of the hypothetical type. More particularly is this so when it is realised that the ever-present spiracular trunks lie between the dorsal and ventral longitudinal tracheæ, when the two latter are both present. Further, whilst there is some evidence to show that the basal connections of the principal tracheæ tend to migrate in a posterior direction, the trachea which is attached to the base of the cubital in many termite species and which precedes the median rib of the wing is not necessarily a migrant medial trachea. Where this condition occurs, the evidence all goes to show (a) that the medial trachea has disappeared and (b) that there are two principal cubital stems (see, in particular, *Microtermes incertus*, Section IX *g*).

The theory of specialisation proposed by the authors (Comstock and Needham) is rather arbitrary. Specialisation by addition takes place only by "a multiplication of the number of the branches of the principal veins," whilst specialisation by reduction follows the atrophy and coalescence of veins. "In nearly every case," they state, "we found the reduction of the pre-anal area accompanied by a similar tendency in the anal area, or, if a reduction has not taken place, there is no increase in the number of veins in this area, the tendency being towards the production of a fewer-veined wing." It is enough for me to add that there is nothing throughout the work under reference bearing upon specialisation by reduction which the ontogeny and final condition of the termite wing does not seem to confirm. But the venation of the termite wing is such that it cannot be derived from the hypothetical type except by methods that are difficult and unacceptable. If anything, the study adds to the palæontological evidence and supports "the quite generally accepted view that the primitive insect wing had many wing veins" (C. & N.)

III. THE NOMENCLATURE AND NUMBERING OF THE WING-RIBS.

The two systems of naming and numbering now proposed rest upon evidence which will be given in a subsequent section. In introducing them here sequence has been subordinated to other considerations, it being impossible to proceed without a recognisable nomenclature. The notation is secondary to the nomenclature, and is suggested to meet the frequency with which certain principal tracheæ, and, therefore, certain principal ribs are duplicated. Upon the whole both systems indicate that there is no fundamental difference between the venation of the termite wing and the wings of other generalised insects.

O. Costa.—The costa of common acceptance. The term is employed to describe that part of the ambient which is modified into a chitinated and stiff rib for the support of the outer¹ margin of the wing. (Exceptionally, as in the hind wings of *Calotermes* and *Cryptotermes*, the costa may be composed of costa and post-costa.)

I, Ia. Post-costa.—This is an obsolete term reintroduced to describe the first auxiliary, a reduced principal rib. The term distinguishes it from the second auxiliary or sub-costa. The post-costal trachea is probably often homologous with the simple costal trachea of Comstock and Needham, where it appears—as in the case of the hind wings of *Calotermes* and *Cryptotermes*—to precede the costa.

II, IIa. Sub-costa.—This rib is: (1) the radius of Holmgren; (2) Desneux's principal branch (R. 1) of the radius; (3) Hagen and Sjostedt's branch of the sub-costa.

III. Radius.—This is: (1) the radius of Desneux; (2) the radial sector of Holmgren; (3) the sub-costa of Hagen, Sjostedt, and others. The pre-existing trachea of the rib, in such generalised forms as *Hodotermes* and *Calotermes*, very greatly resembles the condition found in the cockroach.

¹ The termite wing is regarded as possessing only two margins, an outer and an inner.

IV, IVa. Media.—This term is applied, conservatively, to the rib which succeeds an independent medial trachea.

V, Va.—Cubitus.—This is the cubitus or sub-media of general acceptance. It corresponds with the branched Cu. I of the cockroach. In the wings of certain species it is duplicated, and then the anterior stem (Va) precedes a sub-media rib, which will be called the pseudo-media, as in certain respects it imitates a true media.

VI, VIa. Anal.—The anal of general acceptance.

Hitherto, the names given to the principal ribs of the termite wing have not been based upon ontogenetic considerations, and this will explain the decided differences in the accompanying table, into which Comstock and Needham's nomenclature has been introduced for purpose of comparison.

Nomenclatures: Table of Comparison.

Suggested.	Comstock and Needham.	Desneux.	Holmgren.	Hagen and Sjostedt.
O. Costa . . .	Costa	Costa	Costa	Costa
I. Post-costa . .	—	Sub-costa	Sub-costa	Sub-costa
II. Sub-costa . .	Sub-costa	R. 1.	Radius	
III. Radius . . .	Radius	Radius	Radial sector	Media
IV. Media	Media	Media	Media	
Va. Pseudomedia .	Media	Media	Media	Media
V. Cubitus . . .	Cubitus	Cubitus	Cubitus	Sub-media
VI. Anal	Anal	Anal	Anal	Anal

The earliest of these nomenclatures was probably that of Hagen, and it seems to rest upon the condition of the more specialised wing.

A decided improvement in naming the wing-ribs was introduced by Desneux. He did not recognise Hagen's sub-costa as such but as the radius; and he called the first auxiliary "sub-costa" and the second auxiliary, "the principal branch of the radius," or R. 1.

My own studies of the final tracheal arrangement in *Hodotermes*, *Calotermes*, and *Cryptotermes* led me

to at first regard the second auxiliary as the principal branch of the radius, but the following features convinced me that it is a principal: (a) the regularity with which the preceding trachea develops before any normal branches of the radial trachea arise; (b) the coinciding of its branching (when it does branch) with the branching of the radial and other principal tracheæ; (c) the fact that it has occasionally been found in a duplicated condition (in *Calotermes*); (d) the occurrence of a gradual modification from a branched rib to complete atrophy.

Holmgren attached sufficient importance to this rib to name it the radius; this supports my view that it is a principal. Radius is, however, an unfortunate misnomer for the rib in question, and the application of the term radial-sector to the true radius is inapt.

IV. THE TERMITE WING.

In being deciduous the termite wing possesses a striking character absent from the wings of all other insects. In textbooks it is usually stated of both ants and termites that they "shed" their wings, but the two cases are not analogous. A part of the termite wing is shed, whilst a part is permanently retained. For the permanent part there is no better term than "wing-stump," and to the temporary region (the blade with which the air is sculled in flight) "lamina" is applicable.

These laminae I regard as documents whereon is embossed in hieroglyphs much of the early history of the termite wing-ribs. It seems to me that the provision for shedding the expanded part is, if not original, indeed very ancient; and that the habit of casting a part was acquired when the venation was in a primitive, unspecialised condition. Hence the laminae preserve evidence of a condition that must once have prevailed. As a Rosetta stone was needed for the correct interpretation of the writings of Egypt, so only by looking into the development of the wing can the evidence

supplied by the venation be unravelled and its significance appreciated.

For the transverse suture that cuts across the base of the wing and sharply defines the wing-stump from the lamina, the term "line of fracture" seems most appropriate, as it is here that the lamina breaks away from the stump when the wing is bent, whether artificially, accidentally, or by the muscular effort of the termite.

The ultimate function of the wing-stump seems to be that of protecting the membranous wing-socket throughout the long life of the imago. According to its extent, or according to the degree to which it is chitinised, it reveals or conceals the basal arrangement of the venation. In some species, therefore, its characters are helpful, in others confusing.

In the majority of species the stumps of all four wings are relatively small and sub-equal; in others, those of the fore-wings are proportionately quite large. The first condition is characteristic of the more specialised termites, the second is only met with among the more generalised; but, as certain of the latter (*Hodotermes*, etc.), exhibit the first, there is really little to indicate which of the two conditions is actually the more primitive. The length of the stump is regulated by the distance from the hinge of the wing at which the fracture line develops, but what governs this distance cannot be stated. Where the stump of the fore wing is considerably the larger—as in *Calotermes* and *Cryptotermes*—the atrophied anal field is within the stump, whereas it is partitioned in the hind wing, the fracture crossing the curved or oblique furrow which demarcates the anal field.

The fracture is due to an abscission forming quite late in nymphal life. If its ontogeny is not strictly analogous to the cell wastage leading to the falling of a leaf, it may be compared to what takes place with those plants in which the petioles are cut across at some distance away from the base so that, on the leaves separating, the base of the petiole is left attached to the stem. The development is not connected with any tracheal deviation, as has been suggested.

The anal furrow appears as a crease or fold after the final moult.

V. THE RESPIRATORY SYSTEM.

Plates III to V, figs. 2-48.

As the wing tracheæ develop from tracheæ of the body, their genesis and growth and their diversified development may be better examined with some knowledge of the stem from which they spring and of tracheal growth and development occurring before they are produced. This involves a study of the respiratory system and its development. Naturally, the oldest tracheæ are those present in embryo; but, as these were not easily observed, the very young nymphs were examined.

It was my intention to base this chapter upon the tracheæ of the youngest forms of either *Calotermes durbanensis* or of *Cryptotermes* *sp.*; but in them the cardinal natal stem and its immediate development are too complicated to follow and to describe, although they can be understood with a knowledge of the simpler stem of the *Metatermitidæ*. Subsequently (Section V, f), a short comparison is furnished which deals with the points of difference found between the two forms. The present account relates to the simpler stem and some of its simpler post-embryonic developments, as observed in *Termes natalensis*, *Odontotermes latericius*, *O. badius*, *Microtermes incertus*, and *Eutermes* (*trinervius* group).

When these insects emerge from the egg they are provided with a respiratory system resembling a long, narrow crate, with ladder-like sides and bottom, with an open top and ends and possessing a few paired extensions. The whole is remarkably destitute of branchlets, and there are none of those arborescent tracheæ which develop later, and, to a great extent, shroud it.

The air enters through ten pairs of spiracles, two thoracic, and eight abdominal, and from the spiracles it passes into the

system through short tracheal pipes.¹ Within the spaciousness of the head and the narrow confines of the neck and prothorax, the system is considerably modified; however, it is not independent of the rest, and the homologies of many of the parts there found with those of the thorax and abdomen can be determined, notwithstanding the very different appearance they present.

VA. THE POSTERIOR OR BODY SYSTEM.

Plate III, figs. 2-13.

Considered apart from the head, neck, and prothorax, the system posterior to the first pair of thoracic spiracles may be said to be composed of four longitudinals connected by two series of vertical and one series of transverse commissures. For convenience the longitudinals will be distinguished as the paired dorsal and paired spiracular trunks. There are no ventral longitudinal tracheæ. The upper pair, or dorsal longitudinal trunks, take an undulating course below the sides of the dorsum, extending from the prothorax to the caudal segments. The lower pair or spiracular trunks lie within the sides of the body against the spiracles, and are composed of a series of loops which link up the pipes in a somewhat indirect manner. Each spiracular trunk is connected with its corresponding dorsal by a regular series of palisade or vertical commissures, and the two spiracular trunks are directly connected by an equally regular series of ventral, transverse commissures. The extensions are: (a) the tracheæ of the second and third legs; (b) the ingrowing or visceral tracheæ, arising from each of the last six pairs of palisade commissures; (c) buds of arborescent tracheæ, set almost regularly along the dorsal trunks; and (d) paired buds and twigs upon the ventral commissures.

The examination of the arrangement in nymph after nymph, a small point here and another there, leads to the

¹ The term "pipe" is here used to distinguish the air passage leading directly from each spiracle.

interpretation that the primitive abdominal region is built up by the sub-division or outbranching of the pipes. Each pipe seems to have given off three tracheæ: *a.*, an ascending vertical, *b.*, a descending transverse, and *c.*, a horizontal, fig. 2 (Pl. III). These three tracheæ appear to develop their courses as follows:

Each ascending vertical, on reaching the roof of the body, dichotomises, its two branches take a horizontal direction, *a.a.*, fig. 3 (Pl. III), one extending backwards, the other forwards. Each meets and anastomoses with the corresponding branches of the vertical tracheæ of the next spiracles.¹ Thus is formed on either side of the body a palisade of arches, the bows forming the dorsal longitudinal trunk tracheæ. The caudal branches of each ascending trachea of the last abdominal spiracles grow as a cauda to each dorsal longitudinal trunk, fig. 4.

Each descending transverse trachea, on reaching the floor of the abdomen, crosses it, and thereby meets and anastomoses with the corresponding trachea of the opposite spiracle, fig. 5, and so a ventral commissure is formed.

Each horizontal trachea extends forward, *b.* of fig. 6, until it anastomoses with the descending trachea of the spiracle anterior to that from which itself arose. Thus are formed the spiracular longitudinal trunks, fig. 7. There being ten pairs of spiracles there are ten pairs of pipes, ten ventral commissures, ten pairs of vertical (or palisade) commissures, and nine sections to each spiracular trunk.

This simple segmental arrangement in the abdomen becomes more modified in the thorax.

The tracheæ of the second and third pairs of legs, fig. 9, are attached to the spiracular trunks where these traverse the

¹ "The term "spiracle" is here used to include the stoma, occluding apparatus and tracheal pipe. This is justified upon ontogenetic grounds, as it will be shown that the stoma, to which the term "spiracle" is legitimately applicable in the adult insect, is a transformation of the occluding apparatus, and in certain distended queens the "spiracle" is but a remnant of the pipe.

meso- and metathorax. They are Y-shaped, and the stem of the Y has arisen by the coalescence of the two tracheæ forming the arms. Further evidence of this is found in the temporary separation of the two (*x.x.*) within the tibia.

The six pairs of visceral tracheæ take an inward and then cephalic course, and as each pair traverses the whole of two sections the anterior pair enter the region of the metathorax, *x.x.*, fig. 10.

On the dorsal longitudinals, paired buds *x.x.x.x.*, etc., fig. 11, occur almost regularly upon each section or arch and later develop into arborescent tracheæ, fig. 12, which extend transversely under the dome of the dorsum, towards the median region.

Upon the first, third, and fifth to tenth commissures there are two buds, on the second there are four, and on the fourth there are none, fig. 13.

Vb. THE CEPHALIC AND PROTHORACIC SYSTEM.

Plate III, figs. 14-19.

The stem within the head, neck, and prothorax lies before the first pair of spiracles, and these aerify it, figs. 18 and 19 (Pl. III). Its most conspicuous feature is a great U-shaped trachea which projects through the prothorax, neck, and occipital foramen, and lies close to the floor of the head, fig. 14. This is an anastomosis of the cephalic terminals of the two spiracular trunks, but may owe its origin to the linking up of the terminals by a transverse commissure. From the dorsal surface of each stem of the U just anterior to the spiracles and within the prothorax, arises a large dorsal trachea (marked *x.* in figs. 14 and 15). Each dorsal accompanies its corresponding stem of the U-shaped trachea through the neck and foramen, each then ascends into the dome of the head, and, extending forwards, terminates (*y.*, fig. 15) in the tip of an antenna. Each is again connected, or braced, within the head, to the U-shaped trachea by a vertical commissure (fig. 15, *z.z.*). These two upper

tracheæ are the cephalic terminals of the dorsal longitudinal trunks.

The extensions of this part of the respiratory stem are :

(a) The tracheæ of the first pair of legs, fig. 16. The basal attachments of these are simple; they are linked together by a transverse commissure traversing the floor of the neck, the cervical commissure (*c.c.*, fig. 16).

(b) The paired tracheæ of the anterior lateral extensions of the prothorax (*a.a.*, fig. 17). These are somewhat insignificant and arise near the base of each of the upper main tracheæ (*x.x.*) between the spiracle and the point at which the dorsal longitudinal of the body (*b.b.*) is attached.

(c) The tracheæ of the vertex (*d.d.*, fig. 17) and of the genæ (*c.c.*). They arise in the order mentioned from each of the upper main tracheæ shortly after these enter the head.

(d) The paired complexi of the frons (*e.e.*, fig. 17), each complex being a bunch of three dichotomised tracheæ. A complex is attached to each of the upper tracheæ above the point of attachment of the vertical commissure (*z.z.*).

(e) The paired tracheæ of the lower mouth-parts and the paired tracheæ of the labrum, figs. 18 and 19. These emerge in the order mentioned from each stem of the U-shaped trachea. Each trachea of the lower mouth-parts subdivides into three stems. Of these, the innermost stem travels forwards and subdivides into three branches, one branch entering the glossa, another the paraglossa, and the third the labial palpus. The middle stem behaves likewise, its three terminals resting in the lacinia, the galea, and the maxillary palpus. The outermost stem enters the mandibles, extending to the apical tooth and giving off two side branches, one to the cutting and one to the molar region. Each trachea of the labrum travels upwards to the region of the clypeus, and there bears a complex or bunch of three tracheæ, and then enters the labrum, extending along the margin of this part to the apex. Fig. 18 has been prepared from a cleared preparation, and shows all the visible tracheæ as seen from below, the nearer tracheæ being shown in solid black and

those travelling to the dorsal region lightly shaded. Fig. 19 shows a side view from below, and is also drawn from a cleared preparation of the head of a newly-hatched nymph; in this figure the tracheæ of the parts upon the further side of the head are omitted. It also illustrates the linking up of the cephalic with the body system.

Vc. THE SPIRACLES.

Plate V, figs. 22A-45B.

The spiracles or stigmata of an insect are defined as openings in the body-wall through which the air passes into the tracheæ. Such as are permanently open are regarded as the more primitive or generalised and those with lips as secondary or more specialised. In the case of both types, any occluding apparatus that may occur is said to be internal; e. g. a piece of mechanism intervening between spiracle and tracheal pipe. In all the species that I have examined such bivalvular types as have been met with have the valves partly external and partly internal, one folding slightly over the other to close the orifice. Moreover, when abdominal, such spiracles are but modifications of an occluding apparatus which formerly (in the nymphal stages) intervened between a fixed opening, or pore, and the pipe. For this reason it is proposed to refer to the apparatus from pore to trachea as the "spiracle," whatever condition it may be in; and the remarks, upon the structure, mechanism, and development which follow, relate to *Termes natalensis Haviland*, unless otherwise stated.

As the greater interest attaches to the abdominal series, the spiracles of the thorax have not been examined with particular attention. It may be said of them that they exhibit a simple bilabial form in the nymph and have no remarkable metamorphosis. In the adult the first pair is smaller and different from the second, the latter being shaped like a pair of buttocks. Both retain something of their labial form, figs. 38A, B, C (Pl. V). They are, however, valvular and

closed and opened by special muscles. The tracheal pipes of which they are the mouths are united to them by a short tessellated rim and undergo changes in appearance as growth proceeds, changes which do not affect their tracheal character although transforming them into air-reservoirs. The anterior reservoirs assume a bottle-shape and the hinder become cordiform. Fig. 22A (Pl. V) is a sketch of the juvenile condition found in *Microtermes incertus* and its development is shown in figs. 22B to E. All the sketches are from individuals of the same species and all except E are drawn to the same scale, E being represented on a smaller scale. The tracheæ shown in part are: 1, the dorsal; 2, the spiracular of the prothorax and head; 3, the trachea of the first leg; 5, the passage to the second spiracle; and 4 is the ventral commissure which issues from the base of 5 to which it is attached on the visceral side of the air-sac. Figs. 22F, G, H represent the development of the pipes of the second spiracles in a less number of stages. The stage shown by 22F accompanies the development shown by figs. 22A, B, C; 22G accompanies 22D; and H accompanies E, but is drawn on a large scale. The tracheæ shown in part are: 1, the passage to the first spiracle; 1a, the passage to the third (or first abdominal) spiracle; 2, the palisade commissure to the dorsal-longitudinal; 3, the ventral commissure. This development applies equally well to that of *T. natalensis*.

Considered as a series, each pair of spiracles may be referred to by a number; thus the two thoracic pairs become I and II and the abdominal eight III to X. Briefly stated, III to X of the winged female of *T. natalensis* are bivalvular structures which are the final form of the post-embryonic type, III being more advanced than the rest. The bivalvular form of III of the female is only arrived at by III of the winged male; in this sex the remainder, IV to X, are arrested in a stage closely approaching that exhibited by the whole abdominal series in the nearly mature female nymph. The soldiers and workers display a slightly less advanced form, somewhere between the spiracle of the young and that of the

nearly mature male nymph. In the case of the queen of *T. natalensis* and also the queens of *Odontotermes spp.*, there is a post-adult change in spiracles IV to X which may be described as a disruption of the organ, the valves being torn asunder. In mobile queens, those that have the free run of the hive, such as *Eutermes* (*trinervius* group) and *Hodotermes viator* and others, this disruption does not occur. It may also be mentioned here that in winged females of *Hodotermes spp.* the whole series III to X attain to an equal condition, fig. 35, and in the male, IV to X attain to a stage somewhat more advanced than that of the winged male of *Termes natalensis*. Compare figs. 36A, B, C with fig. 31A. The thumb-like process or bracket of the resister is a very pronounced development in *Hodotermes*.

For a considerable period of nymphal life, the spiracles of the abdomen are more or less unchanged. In the newly-hatched young, this organ (measuring approximately 0.08 mm.) looks like a little pitcher with a long neck and a round mouth. The mouth is the pore, the neck the atrium; and the ascidium, as it may be called, is the lever. Each spiracle lies in a dorsal position within the rolled-in edge of the tergite, and its long axis is parallel to that of the body, the pore facing backwards; and, except in the adult female (series IV to X), the caudo-lateral corner of the tergite forms a hood over it. Lying as it does, it has four aspects: a dorsal, a ventral, an internal or visceral, and an external. Upon the visceral side there is an outlet, formed by the separation there of the atrium from the ascidium; through this the air passes from the spiracle into a short membranous tube, and from this into the mouth of the pipe. Since the pipe is directed downwards and outwards it slants towards the spiracle and makes its union with it somewhat at a right angle. At the base of the atrium there is a vestige of a small plate. The spiracle and its connections, therefore, comprise the features shown in fig. 23A.

Taken separately, these may be described as follows:

- (1) The pore or stigma; a circular opening surrounded by

a stiffened rim which is inserted into the cuticle of the body-wall.

(2) The atrium ; an elongate and wrinkled cylindrical tube distended at the pore by a more or less regular tessellated framework of a hexagonal pattern ; the approximation of the strands forming the heavier chitination of the rim of the pore, fig. 37 (Pl. V). At the end of the atrium, on the visceral side, is a small plate (2a) which is the "resister." The atrium seems to lead directly into the ascidium of the lever.

(3) The lever ; this lies exterior to the trachea and has every appearance of being a simple membranous sac ; but, as it is rigid, only its visceral side can be membranous.

(4) The epi-trachelos ; a small membranous tube whose mouth surrounds the opening between atrium and lever and through which the air passes into the trachelos. It is the mouth of the epi-trachelos which is closed by the bending of the lever towards and across the resister, fig. 23c.

(5) The trachelos is the hexagonally tessellated and bulbous foot of the tracheal pipe.

The developments which first take place are more or less concurrent. The lever gradually loses its vesicular form and so changes to a plate which is slightly concave on the visceral side and convex on the external side. Figs. 25A, B, C represent the lever in vertical section and show what appears to take place. The resister of the atrium develops a deep hiatus, the hiatus arising from the ingrowing of the lower median region, which now protrudes into the lumen, figs. 26A and B. The region of the atrium adjacent to and anterior to the resister becomes prominent and chitinated, forming a "chin-plate" (*ch.*, fig. 30). The epi-trachelos is absorbed into the trachelos which extends and reaches to the opening between atrium and lever. These changes produce the spiracle of the second stage with its quoit-like rim, figs. 24A and B.

The opening and closing of the lumen is brought about by a band of muscle. This has three fixed insertions, the first is to the chin-plate (*ch.*, figs. 28A and 30) slightly anterior to

the resister; from here it passes diagonally to the tip of the lever; from the lever it extends outwards slightly and is fixed to the tergite just within the cephalo-lateral corner, on the line where the chitinisation begins to be less dense. The strap of muscle from chin-plate to lever contracts and draws the lever towards and somewhat across the foot of the resister. The resister and lever are linked by a flexible band which acts as a fulcrum but not as a spring, the lumen being opened by the strap of muscle extending from the lever to the tergite.

The transitional conditions between the second and the third stage differ mainly from the second in the noticeable decrease in the length of the atrium. The shortening of the atrium is a gradual process due to the throwing off of the rim of the pore at each ecdysis. Fig. 30 shows a spiracle about to enter upon the third stage, and a new rim (*nr.*) is seen in the course of formation behind the pore (*pr.*). Another feature is the marked differentiation of the chin-plate.

The spiracles IV to X of the male may be taken as representing the third stage. This form is shown, fig. 31A, from the visceral aspect, and the attitude of the lever when open and shut is indicated below the fragment of the trachelos. In the illustration it will be noticed that the resister has become strongly compressed and that the chin-plate has acquired an auricular form; it is almost transparent, but possesses a chitinated margin. The lever, it will be observed, has suffered no reduction.

Fig. 31B illustrates diagrammatically the external and 31c the dorsal aspect of the organ, the atrium being separated from the closing apparatus. These two figures are designed to show what happens in the case of spiracle III of the male and spiracles III to X of the female, the whole of the atrium being thrown off excepting the chin-plate and resister. This leaves the interior surface of the chin-plate exposed on the body surface and also the anterior edge of the lever, so that these parts now form the valvular pore or stigma. The resister is further reduced and forms one edge of the mouth of the

spiracle. Fig. 32 represents spiracle III and figs. 33 and 34 show the form of spiracles IV to X of the female and illustrate the reduction of the lever.

In fig. 32 the resister (*R.*) is reduced and to it is attached the visceral edge of the trachelos (*m. tr.*) and it still performs its original function of closing against the much modified but strongly developed lever (*L.*), behind which the trachea is seen. The chin-plate (*C.*) is fixed in the cuticle of the body-wall. The occluding muscle (*oc. m.*) still extends from it to the lever and the extensor muscle (*ex. m.*) to the margin of the tergite.

The spiracles of the queen, being more of the nature of tracheal development, are dealt with in the next section, Vd. The condition seems due to the great distension of the conjunctiva, but this does not explain it wholly, as the tearing away does not occur in other queens, which enlarge considerably. The elongate depressions that result have many pits in them, like ear-holes, and into these many tracheæ open freely.

Vd. TRACHEAL GROWTH AND MODIFICATIONS.

Considered apart from the cardinal stem of the respiratory system, the growth and development of tracheæ is tree-like. A trachea grows indeterminately or with a marked tendency to dichotomise. It sends out branches which behave similarly. As the branches increase in length and number, the stem enlarges as does the trunk of a tree. In their ramifications the tracheal course is, on the whole, like that of a root in the soil; with most, however, the field of growth is controlled and a particular region is invaded, but the detail of movement appears ungoverned. This is illustrated by the arborescent branches of the dorsal-longitudinal trachea in fig. 12 (Pl. III), and in the branching of the leg-tracheæ, fig. 39 (Pl. V).

One of the outstanding developments occurs in the case of the pipes of the abdominal spiracles of the female. These are originally simple tubes subdivided into three, as described in Section Va. As the nymph develops, a great number of

individual tracheæ arise, figs. 50A, B, C (Pl. VI) ; from each pipe these grow as in figs. 41 and 42 (Pl. V), and the majority of them travel to the paired ovarian cords which lie within the pluræ. To these they attach themselves like the tentacles of an octopus and form great brushes, figs. 43A, B (Pl. V). This development follows a considerable distension which first takes place at the junction of the three primary subdivisions of the pipe as illustrated in fig. 40 (Pl. V). This phase is succeeded by those shown in figs. 41, 42, and the final nymphal form is that illustrated in figs. 43A, B; A showing an external and B an internal view. In B are to be seen the two muscles behind the spiracles, and below the ovarian cord a part of the peristaltic ribbon is also shown. In these figures it is seen that tracheæ now extend down the pipe and enter a short, broad dilatation. The transformation of the spiracles has already been explained, and the disruption in the case of IV to X of the queen mentioned. Fig. 44 shows a side view of one of this series of spiracles, and it will be noticed that all the tracheæ now open into the cup-like mouth of the pipes. With disruption the valves are shredded to fragments, and the trachelos or mouth of the pipe is now the spiracle, the nature of which is illustrated in figs. 45A and B.

Tracheæ may be modified by the volume of the air-route. In the following section, wherein an attempt is made to homologise different parts of the system, use is made of this feature to explain the disguised bases of a number of palisade commissures. For example, in the nascent stage whilst the pipes of spiracles V to X divide into three principal stems, one of these stems, instead of appearing to be a palisade commissure, seems to be the visceral, with the palisade as a vertical growth therefrom. This change in the arrangement (see fig. 10, Pl. III), is due to the enlargement of the direct route to the part demanding the greater supply of air.

Ve. THE HOMOLOGIES OF THE MAIN STEM.

In figs. 18 and 19 (Pl. III) and 20A and 20B (Pl. IV), an attempt is made to show the natural arrangement of the

nascent stage of the respiratory system. Of the four, fig. 20B is an external aspect of the arrangement upon the left side of the body, and forms the basis of the diagrams used to illustrate the homologies. Fig. 20A (Pl. IV), is more or less diagrammatic (see Explanation of Plates).

It is not difficult to resolve the system of the trunk into a regular scheme by alterations of a minor nature; the abdominal spiracular loops are straightened to accord with their appearance in the winged imago, wherein they seem to stretch taut from spiracle to spiracle; the series of palisade and ventral commissures are also altered to accord with one another, the two palisades of the thorax being somewhat lengthened to agree more in height with the rest. Thus, the system of the head, neck, and prothorax can be first resolved into the scheme given in fig. 46 (Pl. V), in which it is shown connected with the trunk system. This rearrangement of the tracheæ enables us to see (1) that the basal part of the cephalic dorsal (or antennal) trachea is a palisade commissure that has been thrown down and inflated; (2) that the anterior vertical commissure (connecting the dorsal trachea with the stem of the great U-shaped trachea) may be regarded as a palisade commissure, and that the stem of the U is the continuation of the spiracular trunk. The first inference to be drawn is that the arch of the U is a modified ventral commissure. If this is the case, then there are two pairs of palisade commissures, and, counting the cervical as one, two ventral commissures which are not associated with spiracles. On this it may be assumed that two spiracles have been lost to the system. It is obvious that the meso- and metathoracic leg-tracheæ, fig. 9 (Pl. III), owe their Y-shaped form to the anastomosis of two tracheæ. In view of the separation of the tracheæ in the tibia of the front leg, fig. 16 (Pl. III), it is reasonable to assume that the base of this was also composed of two tracheæ. The commissure of the neck connects the tracheæ of the first pair of legs some distance below their attachment to the spiracular trunk; but it is not unreasonable to suppose that it was originally attached to the spiracular

trunk as are other ventral commissures, and that its bases have fused into the leg-tracheæ. If, then, the tracheæ of the mouth-parts are directed ventrally, they correspond with the leg-tracheæ. These alterations appear in the diagram fig. 47 (Pl. V). This diagram illustrates that (*a*) the trachea penetrating the anterior lateral and dorsal extension of the prothorax corresponds with the visceral trachea of spiracles V to X, and is not a wing trachea, as might be readily supposed; (*b*) the trachea of the antenna is the homologue of caudal trachea. The tracheæ of the gena and vertex are probably analogous to the arborescent tracheæ which develop from the buds of the dorsal longitudinal trunk. The difference is that there are two instead of one, but it frequently happens that two arborescents arise from a section of the trunk, and it is not altogether rare for one section to be budless and one or the other of those adjoining to possess two buds.

The complexi of the frons and of the clypeus appear to be without homologues.

Although the visceral tracheæ are regularly confined to the palisades V to X, occasionally, and as a later development, an analogous branch may arise from palisade IV; this is included in fig. 47 (Pl. V).

From fig. 18 (Pl. III) it will be seen that the tracheal twigs which enter the glossæ, paraglossæ, and labial-palpi have their homologies in the twigs entering the laciniaë, galeæ, and maxillary-palpi. Further, the tracheæ of the mandibles are homologous to those of the labial mouth-parts inasmuch that each extends to the apical tooth, and sends one branch to the cutting region and another to the molar region of each mandible. In this connection it may be mentioned that the mandible of the nymph of a *Eutermes* (*trinervius* group) strikingly exhibits three well-defined regions; the apical tooth being the homologue of each palpus, the cutting region of the galea and paraglossa, and the molar region of the lacinia and glossa. (See inset on Pl. IV.)

Vf. THE CALOTERMITE STEM.

Plate IV, figs. 21A, B, C.

The respiratory system possessed by the young of *Calotermes* and *Cryptotermes* on leaving the egg is more ample and more complex than is the *Metatermite* form. Moreover, it becomes more complex as growth proceeds. Apart from this, various structural features—especially the sculpture of the head and the compression of the thorax—alter the courses of the tracheæ, produce unusual post-embryonic developments, and make its detailed examination more difficult.

For the purpose of this section it will be sufficient to compare briefly the system of *Cryptotermes* with that of *Termes natalensis*. The first difference to be noted is the presence of an extra pair of longitudinal tracheæ which lie along the floor of abdomen and thorax, fig. 21A (Pl. IV). These may be said to be composed of a series of loops linking up the ventral commissure, and extend from the commissure of the first to that of the tenth pair of spiracles, continuing beyond the last in a tail-like form into the ventral caudal region, and so resembling the tails of the dorsal longitudinal trunks. This extra pair of tracheæ is also exhibited by *Calotermes durbanensis*, *Hodotermes spp.*, and by *Rhinotermes putorius*.

In slightly more mature nymphs of *Cryptotermes* there is a striking X-shaped trachea across the floor of the prothorax (fig. 21A). This arises out of the brief anastomosis of the median point of the cervical with that of the ventral commissure of the first spiracles. The two tracheæ are approximated at birth and joined by a short isthmus; they gradually fuse, and later are stretched taut so as to form a regular X. A similar trachea has been observed in *Calotermes*, but it appears to originate differently, and has not been satisfactorily studied.

Except for the extra pair of longitudinal trunks and the X-trachea, the characters of the stem of the thorax and abdomen are agreeable with those of the *Metatermite* form; but the cephalic arrangement is quite different.

The simple U-shaped trachea formed by the extensions of the spiracular trunks into the head is wanting, whilst the continuations of the dorsal longitudinal trunks are more amply developed.

The spiracular trunks projecting into the head cavity each have a tree-like form, and their stems are linked together by a transverse commissure placed well back so as to give an arrangement resembling the letter H. In the region of the labium each trunk subdivides into three principal stems which supply the mouth-parts, fig. 21A (Pl. IV). Upon the whole, their arrangement is like that seen in *T. natalensis*, but the paired tracheæ of the labrum arrive within the clypeus by a more indirect route. They first bend outwards more or less at right angles to the parent stems, travel behind the eyes, and then upwards into the dome, bending sharply inwards to the clypeus; here they turn forward at a right angle and pursue a remarkably straight course into the labrum. They may be said to traverse the inside of the head capsule from their point of origin to where they turn out of the clypeus. As in the *Metatermite* form, so in this the spiracular tracheæ are connected with the main dorsal tracheæ by upright commissures, but these are both very incurved and C-shaped. As development proceeds they become approximated and then fuse at the point of contact to form an JC-shaped combination.

In more mature nymphs of *Cryptotermes*, *Calotermes*, *Hodotermes*, and *Rhinotermes* there is a decided Y-shaped trachea between the two dorsal tracheæ (those which have their terminations in the antennæ), the arms of the Y being attached at the same points as are the vertical C-shaped tracheæ just described, fig. 21B. This middle trachea undoubtedly originates in *Cryptotermes* from two tracheæ, each an inner basal branch of the dorsal tracheæ. These

issue from the stem just where the dorsals enter the head cavity. They have the appearance of having grown together in the embryo, and after anastomosing, one becomes arrested, the other extends forwards and crosses and anastomoses with an out-curved, transverse commissure which connects the two dorsals. This problematic development results in the arrangement found at birth, as illustrated by fig. 21c (Pl. IV). The change of appearance that results later, fig. 21b, is no doubt due to the strain of structural developments, and these draw the middle trachea into a position which is approximately in the longitudinal axis of the head.

VI. THE TRACHEÆ OF THE WING-SAC, THEIR GENESIS AND GROWTH.

VIa. THE TRACHEÆ.

The tracheæ of the wing-sac are outgrowths from those sections of the spiracular trunks lying within the meso- and metathorax, and, with two minor exceptions, they have been found to originate between the bases of the Y-shaped tracheæ of the second and third pair of legs, fig. 48 (Pl. V). The outstanding exception to this rule occurs in *T. natalensis*. In this insect the base of the post-costal is frequently beyond that of the anterior arm of the leg-trachea. In *Hodotermes viator* it was once found similarly situated, but in this species the post-costal is less frequently independent of the radial than it is in *T. natalensis*. The rule holds good for the local representatives of the following genera that have been examined: *Hodotermes*, *Calotermes*, *Cryptotermes*, *Rhinotermes*, *Microtermes*, *Eutermes*, *Hamitermes*, *Cubitermes*, *Procubitermes*, *Promirotermes*, and *Microcerotermes*. The tracheæ have either two or three connections. In the representatives of the genera *Calotermes*, *Cryptotermes*, *Eutermes*, *Hamitermes*, *Cubitermes*, *Procubitermes*, *Promirotermes*, and *Microcerotermes* there are regularly three. To these connections with the cardinal stem it is proposed to apply the terms radial root,

medial root, and cubital root. The anterior is called the radial because the scape continues uninterruptedly into the wing-sac and precedes the rib to which the name radius has been applied (see Section III). In *Calotermes* and *Cryptotermes* the post-costal and sub-costal are regularly attached to the radial trachea, the one to the root, the other to the scape. In those species presenting no post-costal the sub-costal is regularly attached to the radial scape. The middle root is called the medial because it is that of the trachea which precedes the media. The posterior is described as the cubital because the scape enters the wing-sac uninterruptedly and precedes the cubitus; to its base is attached any rudimentary anal that may be present. In *H. viator* there are usually two and occasionally three, in *Termes natalensis* there are occasionally two, more often three, basal connections. When there are two they are the radial and the cubital, and the radial trachea then carries the post-costal and sub-costal, as in the other species, whilst the cubital trachea is in a duplicated condition, the inner stem preceding a typical cubitus, the outer a pseudo-media. When there are three connections, the condition is due to the occasional independence of the post-costal trachea, fig. 78 (Pl. VII), an independence which manifests itself quite erratically in *T. natalensis* as regards any of the four wings of a given insect. At the base of the cubital trachea of *T. natalensis* there is an anal trachea; this does not grow into the wing-sac, however, but turns inwards and enters the thoracic cavity, figs. 182, 186 and 187 (Pl. XI).

In *Microtermes* there are usually two basal connections and occasionally three. When two are present they are as in *T. natalensis*, the cubital being always duplicated (the post-costal appears to be often wanting, but when present is attached to the radial). When three are present the extra one is the medial; thus a wing-sac of the species of this genus may present an independent medial in company with a pseudo-medial and a cubital, fig. 200 (Pl. XI).

In *Rhinotermes putorius* there are three roots; these I

regard as the post-costal, the radial, and the cubital. The post-costal is a shortened trachea whose position is analogous to one of the two independent phases of this trachea in *T. natalensis*. The radial is a simple trachea with a few weak outer branches. The cubital is a duplicated trachea as in *Termes*, *Hodotermes*, *Odontotermes*, *Microtermes*, and abnormally in *Calotermes*. Occasionally the cubital root carries three tracheæ and the more anterior of these may be regarded as the medial trachea (see figs. 165, 166 (Pl. X), and discussion, Section IXd).

VIIb. THE GENESIS OF THE WING-SAC TRACHEÆ.

Plate VI, figs. 49-59.

In any adult termite, the two pairs of equally diaphanous wings extend, when folded, to about the same point. In other words, the hind wings are shorter to a fixed degree than the fore wings. This condition is achieved by the earlier appearance of the fore wings; and it is frequently possible to detect two phases of tracheal growth in the organs of one insect, the tracheæ of the fore wings being slightly older they are usually a little more advanced in growth than those of the hind. Much that is said in this and the next subsection rests upon this circumstance, as, naturally, it has not been possible to examine the continuous development of the wing tracheæ in one insect.

The lateral extension of the meso- and metathorax—the beginning of wing-growth—takes place when the insects are very young, about 1.5 to 2 mm. in length. In *Cryptotermes*, in particular, the genesis of the tracheæ seems to occur before there is any obvious lateral extension. The sections of the spiracular trunk first bulge outwards, and, having assumed this position, buds arise, fig. 51 (Pl. VI), and soon develop into tubercles. In *Cryptotermes*¹ the buds

¹ The account from here onwards of growth of tracheæ refers in particular to this generalised species, and to *Calotermes durbanensis*; any point at which a more specialised species differs is the subject of special remark.

become tubercles which are almost regularly clavate, fig. 52, but in other species they are conical, fig. 53. It is during the development of the buds into the tubercle form that the extensions of the meso- and metathorax become noticeable. With the first marked extension a scape grows from each tubercle, and very frequently on one side of its apex, fig. 54. These three scapes (or stalks) extend into the wing-sac as simple tracheæ and are the radial, medial, and cubital tracheæ; the differentiation between the basal tubercle and its scape soon disappearing. In *Termes*, *Odontotermes*, and *Microtermes* (and presumably *Hodotermes*) the cubital tubercle early assumes a bifid form and two stalks grow from it, fig. 55.

In *Calotermes* and *Cryptotermes* it has been observed that before the differentiation between scape and tubercle takes place, a secondary tubercle forms near the base of the radial, fig. 56, and from this develops the post-costal trachea. At this stage four simple tracheæ occur in the wing-sac. Soon after the post-costal has developed a little, the vermiform bud of the sub-costal appears upon the radial stem, fig. 57, and this grows into a stalk, so providing the wing-sac with five tracheæ. Still later, the anal issues from the root of the cubital, fig. 58, so that there are six simple tracheæ, fig. 59. Not until all have made some growth does any one produce branches.

VIC. THE GROWTH AND DEVELOPMENT OF THE WING-SAC TRACHEÆ.

From the foregoing account it will be gathered that the tracheæ of the wing-sac arise in an orderly sequence. Those first appearing are the ones which normally develop the strongest; that is to say, where there are three roots, the strongest tracheæ are the radial, the medial, and the cubital, and, where there are two roots, the strongest are the radial and the duplicated cubital.

For *Calotermes* and *Cryptotermes*, the preliminary development may be summarised as follows :

(a) The bulging outward of the spiracular (or cardinal) trunk as in figs. 49, 55 (Pl. VI).

(b) Bud growth (radial, medial, and cubital), fig. 51.

(c) Development of buds into tubercles, fig. 52.

(d) Growth of the scape of the radial, medial, and cubital tracheæ, fig. 54.

(e) Appearance of the bud of the post-costal, fig. 56.

(f) Development of post-costal.

(g) Appearance of sub-costal, fig. 57.

(h) Appearance of anal, fig. 58.

(i) The elevation of the extended bow of the cardinal from the horizontal to the perpendicular, fig. 60.

The foregoing sequence of events applies to other species having three basal attachments except that with some *e*, *f*, and *h* do not occur. It also applies to those species of which the wing tracheæ have only two basal connections except that either no medial or no post-costal nor anal develops.

The elevation of the bow of the cardinal, or the lifting of the latter to the plane of the meso- and metanota, is necessitated by the forming of a "shoulder" to the wing-sac. It is accentuated by the downward "drag" of the leg-tracheæ upon it (see fig. 60, Pl. VI).

Ordinarily, where there are three basal connections, that of the medial is closer to that of the cubital than it is to that of the radial, in young nymphs (fig. 52). An opposite state of affairs occurs subsequently and the base of the medial is far removed from that of the cubital, sometimes to a very great extent, figs. 203, 205 (Pl. XI). The change of position is due to a considerable intercalary growth of the cardinal, which occurs between the roots of these two tracheæ. Because of this secondary growth, the scape of the cubital lengthens in proportion to the degree to which its attachment is carried further and further from the mouth of the wing-sac.

A feature of much interest is the behaviour of the trachea that enters the wing-sac behind the radial. This may be the true medial or the pseudo-medial (outer cubital), but its

origin makes no difference to the regular behaviour seen in the wings of more mature nymphs. In all cases, on entering the wing-sac it approaches the radial. In the hind wing it is briefly applied to the radial, bending back again to a median position; in the fore it does not reach to the radial, but recedes and becomes briefly applied to the cubital, from which it bends off again to a median position.

This trait may be taken as evidence that, where there are two basal connections, the base of the medial trachea has migrated to the base of the cubital; but against this is the evidence furnished by the frequent duplication of tracheæ in *Calotermes* and the frequent occurrence of a true independent medial, in the presence of a duplicated cubital, in *Microtermes incertus*. Moreover, in *Hodotermes*, *Termes*, *Odontotermes*, and *Microtermes* both stems of the cubital develop along similar lines; a similarity of development which is most marked in *Hodotermes* and *Termes*.

The subsequent development of the wing tracheæ comprises the following:

(j) The production of main branches—or offsets.¹

(k) The growth, from stems and offsets, of innumerable tracheal fibrils.

In the last nymphal instar the wing-sacs are pervaded with tracheæ—especially those of the more generalised species—and it is by no means uncommon for the principals and their sub-divisions to extend and travel—usually in the direction of the base of the wing-sac—along the edge of the marginal thickening, figs. 78, 94 (Pl. VII); these extensions may also bend back into the body of the wing-sac, fig. 142 (Pl. IX).

Apart from the normal, many cases of apparently abnormal development have been noticed; that is to say, a principal trachea is often duplicated.

¹ It is convenient to apply the term “offset” to the regular series of main branches of the cubitus exhibited by all species, and also to the series of outer branches of the radius possessed by *Hodotermes*, *Calotermes*, and *Cryptotermes*.

The duplication of principals is very frequent in *Calotermes*, where all have been found in this condition except the radial. It is also common enough in *Cryptotermes*.

VI. REDUCTION OF TRACHEÆ.

In the final wings of *Calotermes durbanensis* numerous abnormalities of the venation are directly traceable to pre-existing extra principal tracheæ. As evidence of this is also to be found in the wings of other species, one is justified in concluding that the predecessor of the termite wing was a tracheated organ into which many more principal tracheæ penetrated than is ordinarily regarded as the full complement, and perhaps the production of these exceptional tracheæ may be regarded as reminiscent of an ancient ancestor.

In an earlier section it has been shown that the development of the tracheæ of the wing-sac occurs in an orderly sequence. Making allowance for reduction in area, it is equally true that both the gradual reduction of some principal tracheæ and the loss of others takes place in an orderly sequence; this reduction may be described as a gradual retirement along the line of advance.

Of the principal tracheæ, the sub-costal and the anal are the latest to develop, and should, on the foregoing premises, be the first to disappear. However, as a rule, it is the post-costal that is earliest lost, then the anal, and, lastly, the sub-costal; this slight derangement of the sequence being no doubt due to the narrowing of the basal area of the wing.

The post-costal is quite extensive and many-branched in *Hodotermes karrooensis* and *H. transvaalensis*. In *H. viator* it is weaker and less branched. In *Calotermes* and *Cryptotermes* it is, comparatively speaking, weakly developed and but rarely branched, and is more atrophied in the hind wing than the fore wing. It is a shortened and simple trachea in *Rhinotermes putorius*; reduced and inconstant in *Termes natalensis*; and, in *Microtermes*

spp., it appears as a fine, short trachea, or fails altogether to develop. The sub-costal trachea is often branched in *Hodotermes*; it is more often simple in *Calotermes* and *Cryptotermes*. In *Termes natalensis* and *Microtermes* it is shortened and reduced, fig. 176 (Pl. XI), and in *Rhinotermes* it is missing. In most of the *Metatermitidae* examined it is either absent or very much reduced.

The radial is strongly branched upon both sides in *Hodotermes*. The inner branches or sectors are wanting in *Calotermes*, *Cryptotermes*, and *Rhinotermes*. In all the other species except *T. natalensis*, both inner and outer branches are missing or very much reduced. Thus, in the case of *Rhinotermes* there are very reduced outer branches with no inner. In *Termes natalensis* there is a regular series of outer branches, but ribs do not arise from them in the final wing, and in this and certain *Odontotermes* there is a tendency—possibly due to reversion—for the radial to produce relatively strong inner branches; in some wing-sacs of one and the same insect these are present, in others absent.

When present the anal trachea is much reduced in all the species studied, and in *T. natalensis* it enters the thoracic cavity and not the wing-sac.

A further feature which may be mentioned in this connection is the tendency for the tracheation of the wing-sac, as a whole, to become reduced by the failure of the principals to produce that multitude of fibril-like branches so characteristic of the wing-sacs of the more generalised species, and practically absent from those of the more specialised.

VII. THE VENATION AND UNFOLDING OF THE FINAL WING.

Plate VI, figs. 61–69.

Hitherto, in discussing the nymphal wing, a fairly flat organ has been under reference, and this, when cleared in glycerine jelly, reveals the air-laden tracheæ stretched out

upon a fairly level plane. This condition obtains until the insect has progressed well along the last nymphal stadium. It is then succeeded by a phase in which the tracheæ are found sinuate and later coiled and overlying one another, fig. 61 (Pl. VI). This is due to the growth of the final wing and the lengthening of the tracheæ with it. The cuticle encasing it cannot give way along its margin, but both the upper and lower surfaces bulge outwards, the growing wing accommodates itself to its narrow confines by a series of longitudinal folds and transverse creases, and so becomes packed up very tightly.

From quite early stages pale bands are to be seen in the organ. As the largest of these cause faint ridges to form on the dorsal surface of a wing-sac but leave no other trace on the moulted cuticle, they must represent a certain differentiation of tissue. Their structure has not been studied, but they no doubt consist of modified cells which form about the tracheæ and cause thickenings between the upper and lower cuticles. The principal tracheæ have not been noticed dissociated from them, but this is not the case with some of the branch tracheæ. Consequently, certain pale thickenings are found in which there are no tracheæ. As development proceeds certain tracheæ tend to move out of the thickenings. After such a movement a further thickening may or may not form about the latest course of the trachea and hence one and the same trachea may give rise to two thickenings. Two concrete illustrations may be taken from the wings of *Calotermes durbanensis*.

The first is the frequent presence, in the final wing, of a bicornute branch near the base of the media, lying between it and the radius, figs. 112 (Pl. VIII), 127 (Pl. IX). This rib is derived from a similarly shaped, pale thickening that is occasionally to be seen in a wing-sac, and it depends upon the stage in which the tracheation of the wing-sac happens to be whether this is or is not associated with a trachea. When it is so, the trachea is furcate, with the tips of its branches turned backwards, fig. 62A (Pl. VI); when

it is not, the furcate trachea is present but differently disposed, fig. 62_B (Pl. VI).

The second illustration furnished by the wing of this species is to be found in the field of the cubitus. This, in the final wing, frequently displays more or less interrupted, erratic, or independent ridges between the cubitus offsets, some being ill-defined, others plainly marked. These ridges are due to the pendulum-like swinging of the offsets of the cubital and to the formation of stronger or weaker thickenings about them, in their earlier positions. In short, a thickening once formed tends to persist, and so gives rise either to a ridge or a rib. Figs. 63_A, _B are diagrams designed to illustrate this point. Fig. 63_A represents the first position of two cubital offsets. In fig. 63_B these are seen to have moved forward, leaving the thickening behind. The deserted thickenings become ridges in the final wings, and those occupied by the tracheæ become ribs.

As the final wing develops it forms into longitudinal rolls, and into these is gathered all the tissue. The rolls soon become contorted and vermiform; they appear coiled up and apparently inextricably mixed, fig. 64. In this condition the wing is unsheathed.

However, complicated as the arrangement looks, it is not difficult to see that each roll is the counterpart of a rib that will form in the final wing. In other words, the tissue has centralised along the courses of the thickenings. Inasmuch as the tracheæ also grow one would expect to find them to be the cores of those thickenings that formed latest about them. This is so in part, but not wholly, and the condition seems to be due to the tracheæ not attaining to the same length as do the rolls, and, therefore, not following all the plications.

Well before the final ecdysis, the imaginal wing becomes surrounded by a layer of air which separates it from its sheath.

After the moult, the adult is white and soft-bodied. The wings remain tightly packed, except for the expan-

sion of their basal region. Pigmentation, which synchronises with chitinisation, takes place very slowly and not until after the wings have fully expanded. First the head, then the body and legs, and last the wings become coloured and hardened; the whole process taking place in complete darkness. The pigmentation of the head and of the sclerites appears to begin at a central point and then to spread outwards; that of the wings begins at the roots, and has the appearance of flowing along the ribs and out from them into their branches, whether such branches were preceded by actual tracheal connections or have arisen from the fusion of thickenings forming about approximated or applied tracheæ. For this reason a cross-rib is usually more strongly attached to the more chitinated of the two principals it connects although, ontogenetically, it may be a branch of the weaker. The unfolding and hardening of the wing is a peculiarly slow process. After the last moult, the wings of *C. durbanensis* unfold in the course of several hours—probably three or four—but nearly a full week elapses before the body is fully chitinated and the wings hardened. Throughout the greater part of this period there is a distinct lumen in the post-costa, sub-costa, radius, media, and cubitus and the main offsets of these ribs, whilst a lumen representing the anal trachea lies within the anal field, fig. 68 (Pl. VI). Except the basal branch of the post-costal, *x.*, fig. 68, there is no such lumen in the marginal nor in the cross-ribs, minor branches, and ridges. The lumen is a capillary air-tube from which the air slowly disappears, often giving the effect of a broken column of mercury in the tube of a thermometer. When the wings are first unfolded traces of the tracheæ can be made out here and there, more especially at the bases of the wing, and then the spiral is drawn out, fig. 69. In *Termes natalensis* and allied forms, the expansion of the wing and the complete hardening of the adult seems to proceed much more slowly, and there is some reason to believe that the better part of a month elapses before the adult insect is perfectly developed.

The unfolding and spreading of the wing takes place from the stump outwards, as seen in the nine diagrams, figs. 65A to K, prepared from wings of *T. natalensis*. During this period the insect walks about holding out its wings in the attitude depicted by fig. 66. The process may well be likened to the billowing out of a crumpled and wet cloth by driving a blast of air below it, compare figs. 67A, B, C, D, which represent wings of *T. natalensis* in four degrees of unfolding. In this insect the tracheæ may be found, practically intact, in the wing stumps; but there are no air-passages through the ribs, fig. 67D. The radius, pseudo-media, and cubitus appear, however, perforated by a minute capillary, which is probably ill-defined because filled with a fluid. What seems to happen to the tracheæ is that they are stretched until the spiral is unwound, and are then absorbed; this conclusion is based upon the occasional presence of frayed-out tracheæ in the more apical part that has just unfolded; such were present in the wing shown as fig. 67D. It is very obvious that the minor tracheæ are absorbed, and there is some reason to believe that this takes place before the final ecdysis.

VIII. THE VARIATION IN THE VENATION.

Some reasons have already been stated which will account in part for the variation in the venation and for the extreme variableness of the reticulation.

Final wings differ so much in detail that it is impossible to put aside as quite alike any two, even of one insect. It may, however, be said that the more specialised the species, the more is the venation of one wing agreeable to that of its companion, and, the more generalised, the greater the irregularities. This is largely because the more generalised species have more reticulate wings.

In the preceding section the statement is made that thickenings form about the tracheæ. To this it may be added that the ribs of the final wing are transformed thicken-

ings. The point that the marginal arises from a cuticular thickening which does not form about a trachea has been sufficiently emphasised.

Indeed, for all the rest of the venation it may be laid down as an axiom that where there is no preceding trachea there is no succeeding rib or even ridge. To this it may be added that when the growth of a trachea is weak or when a trachea is undeveloped the succeeding rib is similarly affected. Upon the other hand, it is equally true that thickenings do not necessarily form about all minor tracheæ, and consequently every such trachea does not invariably give rise to a rib in the final hardened wing.

Variations in the venation are mainly to be traced to the variation of the tracheation. This is well illustrated in *Termes natalensis*. For this species it may be stated that the radial may have from 0 to 5 strong inner branches (sectors), the pseudo-medial may be deeply furcate and many-branched or practically simple, the cubital may be over-developed or under-developed. If, of the three, the pseudo-medial is more or less simple, then either the radial possesses sectors or the cubital is over-developed. Usually, if the pseudo-medial is well-developed the radial has no sectors, and the cubital presents either a medium or an under-developed condition. When the radial possesses sectors and the pseudo-medial is well-branched, the cubital is under-developed.

The only other influencing factor seems to me to be the hardening of the wings, to which may be traced breaks and dislocations and actual obliterations. It has to be borne in mind that when finally expanded the termite wing is soft, and days, perhaps weeks, must elapse before it is hardened and rigid. The upper and lower surfaces, never far apart, are drawn closer together, and the process of their union tends to smooth out any rib or part thereof that may be weakly formed. So much is this the case that a branch of the cubitus may lose its basal connection and appear as an independent, from the margin. Obliteration is very marked in *T. natalensis*. In this species the freshly-expanded wing

exhibits, in detail, a reticulation that the pre-existing tracheation has given rise to, but as the wings harden this completely, or almost completely, disappears; the degree differs apparently in different races. The same factor also obliterates that portion of the marginal which extends along the inner edge.

It may be said literally that the final wing mirrors the main tracheæ of the wing-sac with remarkable precision, and, with minor exceptions, it is a fact that the ribs represent the tracheal arrangement. Fused ribs arise from the amalgamation of thickenings. It has been shown that anastomosis may occur within the body of *Cryptotermes* between tracheæ, which touch one another, but nothing of this sort has been found in the wing-sac. Tracheæ may apply themselves closely to one another, or they may cross one another in the wing-sac, but they do not anastomose.

Independent ribs are to be sought for between the offsets of the cubitus. In the *Metatermitidæ* they are usually offsets that have lost their basal connections. In *Cryptotermes* they succeed thickenings forming about the ingrowing tips of cubital offsets, figs. 142 (Pl. IX), 146, 149 and 152 (Pl. X).

The following details regarding the variation of the venation as a matter apart from the presence of extra ribs and other extraordinary conditions, are given in a condensed form. The subject is one that can be considerably elaborated, but to do so would serve no useful purpose. In all instances the results given are based on the examination of the wings of the insects of one nest in one season.

Hodotermes viator (Latreille).

The post-costa is simple, as a rule, but it may exhibit one or two minute offsets to the costa, more particularly in the fore wing.

The sub-costa may also have one or two outer branches; in rare instances there are more than two, and then well-developed.

The radius has both outer and inner branches. The outer branches, or offsets, ordinarily connect with the costa; but one or two, near the apex, tend to extend towards the wing-tip, taking a more or less parallel course with and between radius and costa. The number of offsets is variable, 3 to 6, and any one may be simple or subdivided. The inner branches, or sectors, are variously developed, the more basal being frequently atrophied; when few in number all may reach the inner margin of the wing; when many, most are atrophied. The sectors may be simple or much subdivided; the subdivisions may anastomose among themselves or with the pseudo-media. The sectors present in a wing range in number from 3 to 6, of which 2 to 5 may reach the wing-margin.

The pseudo-media is, exceptionally, simple, fig. 84A (Pl. VII), usually it is deeply furcate; when furcate its two main branches may be simple or subdivided. Its subdivisions may extend to the margin at 1 to 4 points. In some cases the subdivisions are anastomosed to the radius sectors and cubitus, fig. 84c, and occasionally are so absorbed that the pseudo-media may appear as not extending to the wing margin.

The cubitus exhibits a variable number of offsets, 8 to 12, which are either simple, furcate, or more subdivided.

The anal of the hind wing is extensive when compared with the trachea it succeeds, and almost invariably fuses with the basal offsets of the cubitus, figs. 70B (Pl. VI), and 84B, c, D (Pl. VII).

The wings of other local representatives of the genus have similar diversities. Larger wings differ only in that the post-costa displays stronger and more numerous branches, fig. 70A (Pl. VI), and the sub-costa is more frequently branched.

Analysis of ten wings of *H. viator*:

Post-costa: Simple, 7; with one branch, 2; with two branches, 1.

Sub-costa: Simple, 2; with one branch, 6; with two branches, 2.

Radius: With three offsets, 2; with four, 4; with five, 3; with six, 1. With three sectors, 3; with four, 1; with five, 5; with six, 1.

Calotermes durbanensis Hav.

The wing venation of this species is much more variable than that of any other species examined. That the venation also exhibits a wider range of extraordinary conditions has no bearing on the matter of the variability of the venation. A monograph would be required to deal with this subject, its extent being limited only by the number of wings available. Although in many of the wings illustrated on Pls. VIII, IX, the venation is abnormal, they serve very well to illustrate the features here discussed.

The post-costa, independent on the fore wing only, is regularly simple, but it merges into the costa anywhere between one-quarter and one-sixth the length of the lamina.

The sub-costa is generally simple, but occasionally it may exhibit one outer branch. It unites with the costa at any point from one-half to three-quarters the length of the lamina.

The radius possesses 4 to 8 offsets to the costa. These are mostly simple and straight, but they may be variously subdivided or they may be imperfect, or they may anastomose with one another. In 29 fore wings, counting subdivided offsets as one, the average and common number was 7; in 28 hind wings the average and common number was 5; the range was, however, the same for both fore and hind wings. The irregularity of the subdivision of the offsets is illustrated as follows: Of 47 wings, 24 possessed simple offsets, 13 had one furcate offset, 9 had two such offsets, 1 had three and 1 four; the remaining 8 had one offset with two branchlets.

The media is usually simple; it may, however, be furcate or well-branched. In the case of 62 wings (fore and hind) 21 had a simple media, 26 a media with a minor apical prong, and 15 a media more or less well branched.

The cubitus exhibits a variable number of offsets; these are

generally simple, while some may be forked or even more subdivided. The subdivided offsets vary from 0 to 5. Counting subdivided offsets as one, in 31 fore wings the number of offsets varied from 8 to 13, the average being 10 and the common number 12. Similarly, in 28 hind wings, the range and average being the same, the commonest numbers were 10 and 11.

The cross-ribs between media and radius vary widely in number, form, and arrangement. The reticulation between media and cubitus may be represented by a simple ridge, by a feather-stitch, a festoon, or a lace-like pattern. The ridges between the offsets of the cubitus are rarely if ever the same in any two wings.

Cryptotermes sp.

These are interesting little wings exhibiting an erratic arrangement in the outer apical quarter, between cubitus and radius.

The post-costa (fore wing only) has always been found simple and varying only in length.

The sub-costa was simple in all wings noticed, and 52 were specially examined for the purpose.

The radius of the fore wing has 6 to 9, and of the hind wing 4 to 7 oblique offsets to the costa; these are normally simple, only one forked branch being found in 52 wings. The radius of the hind wing may possess as many offsets as that of the fore wing, but generally it has from 1 to 3 less. The common number for the fore wing was found to be 8 and for the hind 6. The following table represents the arrangement for 8 individual insects:

Wing.	Left.	Right.	Left.	Right.	Left.	Right.	Left.	Right.
Fore . .	7	7	8	7	7	8	8	8
Hind . .	5	7	7	7	6	5	6	5
Fore . .	7	7	8	8	7	9	8	9
Hind . .	7	6	5	6	6	6	6	7

An analysis of 20 fore and 25 hind wings gave :

		Fore wings.	Hind wings.
Radius with four offsets .	.	0	1
„ „ five „ .	.	0	6
„ „ six „ .	.	1	12
„ „ seven „ .	.	6	6
„ „ eight „ .	.	9	0
„ „ nine „ .	.	4	0

Not infrequently (20 per cent.) the media possesses a sector that extends in a straight or sinuous course to the apex of the wing; when this is present the cubitus is restricted; when absent, the cubitus is more extended.

Termes natalensis Hav.

The simple radius may exhibit well-defined inner branches or sectors which curve shortly to the apex of the wing. When present the number varies from 1 to 4.

The pseudo-media may be practically simple, that is, with a furcate tip in the apex of the wing; more frequently it possesses 1 to 3 strong inner branches which are simple or erratically subdivided. In 18 wings before me, 6 have the pseudo-media with one, 6 two, and 6 three such branches. In 31 wings where the pseudo-media was found more or less branched, the first branch originated before half the length in 8, at half in 18, and beyond half in 5 cases. In one of these wings two branches originated before half the length. The inner margin of this wing is supported by the branches and the subdivisions of the pseudo-media and the offsets of the cubitus. In order to ascertain whether there was any degree of consistency in the number of points at which the margin was so supported, 12 wings were examined with the following result :



Pseudo-media	2	5	6	6	6	6	6	7	8	10	11	13
Cubitus	29	17	18	20	21	22	27	18	22	25	18	15
Totals	31	22	24	26	27	28	33	25	30	35	29	28

Microcerotermes sp.

In the particular species under reference the wings may be said to have specialised towards a more or less fixed venation. The diversities although small are still frequent. The radius is always simple. The media may be simple or furcate or further subdivided. In 24 wings it supported the margin at four points in 1, at three in 7, at two in 12, and at one in 4. The offsets of the cubitus are, on the whole, simple; one of the series may, however, be furcate. The number of offsets ranges from 8 to 12, the average and common number being 10. None of the wings of this *Microcerotermes* showed any abnormality (24 examined); but, from those of a smaller species,¹ the media was often absent.

Microtermes sp.

In this species, of which 10 wings were examined, the media was usually furcate. In 5 the prongs were short, in the others more profound. When this latter condition occurs each prong may be more or less subdivided, so that the media may support the margin at 2, 3, 4, or 6 points. Occasionally the diversity of the venation is added to by the branches of the media crossing the cubitus. The offsets of the cubitus are on the whole simple; in 5 of the 10 wings, 1 furcate offset was found. In the 5, where all were simple, the number present ranged from 10 to 13.

¹ Probably *M. zuluensis* Holmg.

IX. SPECIAL WING STUDIES.

IXa. *HODOTERMES* spp.

Pl. VII, figs. 78-84D.

The wings of various *Hodotermes* all possess a very similar scheme of venation, such differences as do occur being chiefly the degree of coarseness in which the ribs are displayed. At one extreme stands *H. karrooensis*, fig. 70A (Pl. VI), at the other *H. viator*, figs. 84A to D (Pl. VII). The ribs, in the former species, are not only more gross than those in the latter, but the branching of some, particularly the post-costa and sub-costa, is more ample and the "reticulation" more decided.

The ribs *Pst. C.*, *Sc.*, *R.*, *Ps. M.*, *Cu.* and *A.* are preceded by tracheæ. The costa may not be so strongly developed as the radius, especially towards the apex of the wing, and its continuation around the inner margin is much obliterated. It extends along the outer edge of the wing-stump, but is attenuated or thinned out at the root of the wing.

The post-costa forms the anterior articulation of the wing and extends as a strongly chitinated ridge through the wing-stump into the lamina. It is connected with the costa by a short curved branch or strut, which occurs outside the line of fracture in the fore wing, and inside of it in the hind, and is preceded by a branch of the post-costal trachea, *x.*, fig. 78 (Pl. VII).

The pseudo-media unites in the hind wing with the radius well outside the line of fracture, fig. 70B (Pl. VI). In only one wing has a deviation from this rule been found, and in this, fig. 71 (Pl. VI), its union with the radius took place at the line of fracture. In the fore wing, the pseudo-media enters the wing-stump, there its base merges into the bases of the radius and cubitus, fig. 70A (Pl. VI).

The anal of the hind wing may be described as a prolongation of the somewhat pyriform anal lobe of the stump; it

projects much further into the lamina than one would expect from the atrophied condition of its pre-existing trachea.

It will be noticed, figs. 70A and 75 (Pl. VI), that the sub-costa is as independent of the radius as is the cubitus, in both wings. Apart from variations the wings of *Hodotermes* do not present many abnormalities, and several hundreds have been examined for the few illustrations here given. In the case of *H. viator*: (a) two wings were found in which the sub-costa was duplicated, figs. 72A and 72B; (b) one wing in which it was deeply furcate, fig. 73, a condition that may have arisen from a duplication of the pre-existing tracheæ; (c) one wing with the post-costa deeply furcate, fig. 74; (d) the sub-costa appeared in a strongly-branched condition, fig. 77, unusual for this species. In the case of *H. transvaalensis*: (a) in one wing there was no pseudo-media, fig. 75 (Pl. VI); (b) the pseudo-media occurred in a duplicated condition, fig. 76.

My studies of the tracheæ of the wing-sac have been practically restricted to *H. viator*, and then to the organs of almost mature nymphs. The majority of specimens examined conformed with that illustrated, fig. 78 (Pl. VII). This shows: (a) the post-costal with an independent basal connection (see also fig. 82 and compare with figs. 80, 81, 83, Pl. VII); (b) a duplicated cubital; (c) the anal attached to the stem of the cubital near the fork of the two cubitals. The anal is generally in this position, but may often have a more independent position, fig. 83, and may be decidedly subdivided as in this particular instance.

The abnormalities noticed were: (a) in one wing-sac the inner cubital was much reduced, fig. 79 (Pl. VII), whilst the outer, or pseudo-medial, was strongly developed; (b) in three wing-sacs three tracheæ were attached to the cubital stem (as seen also in *Rhinotermes*), in one of these the outer of the three was considerably atrophied, but in the others, fig. 80, it extended practically to the apex of the wing-sac; (c) in one wing-sac, fig. 81, the post-costal was duplicated; (d) in one wing-sac an extra trachea was found entering the

wing-sac and closely applied to the radial along a part of the length of the latter, fig. 82; unfortunately the basal connections of the tracheæ were broken, and the figure represents all that could be made out.

IXb. *CALOTERMES DURBANENSIS* Haviland.¹

Plates VIII-IX, figs. 38-134.

Altogether between 400 and 500 wings of this insect and quite 100 wing-sacs in various stages of development have been examined. The wing examinations show that, apart from those almost individual peculiarities previously grouped as variations (Section VIII) about sixteen wings in each hundred exhibit a more or less abnormal venation. It may be gathered that a marked variation is characteristic of the species, and not of individual colonies, from the fact that such obtains in five colonies from distinct centres, although the bulk of the total cited was made up of 227 wings from one colony and 165 from one another.

In the tracheation of the wing-sac and in the venation of the wing this *Calotermes* differs fundamentally from *Hodotermes*. In the wing-sac the medial is always present, and normally the cubital is not duplicated. In the wings, the two most striking differences lie (i) in the absence of sector branches from the radius of *Calotermes*; (ii) in the seeming absence of the post-costa from the hind wing, a rib that is strongly defined in the hind wing of *Hodotermes* (compare fig. 86 with figs. 84B, C, D, Pl. VII). Other differences are: (a) the position of the median rib; this, as the true media in *Calotermes*, extends to the apex of the wing and is sub-parallel to both radius and cubitus; (b) the presence of a series of cross-ribs connecting the radius and media; these do not occur, as between pseudo-media and radius, in *Hodotermes*; (c) the noticeable fusing of the media with the cubitus of the fore wing, fig. 85 (Pl. VII), outside the line of fracture.

¹ For the determination of this termite see Appendix.

In the stump of the fore wing the costa and post-costa seem to arise from a common stem. The costa is, however, joined by a branch from the post-costa, see fig. 68 (Pl. VI), and the costa, in a somewhat diminished form, extends around the front margin of the stump. In the hind wing the costa suffers a diminution at relatively the same point so that it enters the wing-stump as a reduced rib, and here, as in *Hodotermes*, the post-costa is one of the chief ridges of the wing-stump. Of all the hind wings examined, the post-costa fused with the costa shortly after entering the lamina, fig. 86 (Pl. VII), with two exceptions. In these it was almost independent of the costa in the laminae, fig. 87 (Pl. VII). In only one fore wing was the post-costa found fused to the costa, and then so that the two formed a "double-barrelled" rib.

The variations of the venation can only be understood and the abnormalities explained by a study of the development and behaviour of the pre-existing tracheae. Much of this has already been alluded to at length in other sections. Attention may here be drawn to the development of the tracheal system as illustrated by the series of camera lucida sketches rendered as figs. 88 to 94 (Pl. VII). The following points will be noticed: (a) the constant presence of the post-costal trachea in the hind wing-sac; (b) the building up of the main system, fig. 93; (c) the secondary development of minor tracheae accompanied by the lengthening of the main series, fig. 94; and (d) the "pot-bound" effect caused by the marginal thickening.

Notice may also be taken of the varied development of the anal or anals. Commonly there is a single simple anal present, figs. 92 and 97; not infrequently the single anal is furcate, figs. 94, 95 (Pl. VII); rarely it is three-pronged, fig. 99A (Pl. VII). Quite often there are two anals, and both may be simple, figs. 93, 98A, or one may be simple and another pronged, fig. 96. Inhabiting an atrophied part, the anal is, in whatever form, atrophied; that, when displaced, it is capable of considerable development is illustrated subsequently.

In comparatively young nymphs one finds abnormal tracheal

departures, and there is no evidence to show that the complicated arrangements, to be discussed, are due to physical injuries. The following series of abnormal schemes are selected to indicate the range of departures from normal development, and are arranged from the more simple to the more complicated.

Fig. 95 (Pl. VII) represents an abnormal medial which has developed two strong branches, both of which accompany their parent stem to the apex of the wing, but cross one another in their progress there. The crossing of tracheæ is very frequent in the case of branches from principals, and principals themselves often cross. In fig. 96 (Pl. VII) the medial is seen crossing the cubital and invading its field. An event of this sort usually leads to the part atrophy of one of the tracheæ, in this case the media, and the over-development of the other. It results in the formation of large elongate cells in the final wing and those illustrated in figs: 118, 120 (Pl. VIII), 125, 127, 128, 130 (Pl. IX) seem to owe their condition to this factor. These wings are much like others, figs. 113 (Pl. VIII), 119 (Pl. VIII), but here the median cells may have arisen from the coming together of tracheæ (as in *Cryptotermes*) and not from crossing.

Fig. 97 (Pl. VII) illustrates a fairly simple case of a duplicated trachea, the medial, and is selected to show extra features; i.e. the crossing of the two and the part atrophy of one. Fig. 98A (Pl. VII) illustrates another case of a duplicated media. It differs from the former inasmuch that the duplication seems a secondary condition, the outer medial appearing as a growth from the inner, fig. 98B (Pl. VII). In this case the two extended through the median field and reached to the wing apex. Fig. 99A shows a simple duplication of the cubital trachea, and fig. 99B how the extra trachea originates opposite the seat of the anal. In this case the two tracheæ maintained a cubital character; that is, both had offsets to the inner margin of the wing-sac, as is the habit of the pseudo-media and cubitus with *Hodotermes* and other species to be mentioned later.

Fig. 100 (Pl. VII) is a rare example of a duplicated post-costal in the presence of a duplicated cubital, and it will be noticed that the inner post-costal has crossed the radial proximally to the base of the sub-costal.

Fig. 101A (Pl. VII) is a remarkable scheme that owes its origin, in the first place no doubt, to the entrance of the cubital into the wing-sac anterior to the medial. In intruding itself into the middle region thus the cubital carried its duplicated anal into a false position and the two anal tracheæ have grown enormously. As a consequence of this there is only one normal trachea, the post-costal, present. An anal intrudes between it and the radius; the radius is reduced to a simple trachea and the sub-costal has failed to develop. The second anal intrudes between the radial and medial and upon the medial falls the aerifying of the outer apical margin. It accomplishes this by developing radial characters, producing a series of three strong outer offsets. The cubital, it will be noticed, crosses back again over the medial, fulfils its normal functions, and at the same time produces two strong branches to aerate the region normally supplied by the medial. Fig. 101B illustrates the connection of the anal with the cubital.

Fig. 102A illustrates the most extraordinary case met with. In this wing-sac three principals are duplicated—the sub-costal, the medial, and the cubital. The outstanding feature of the scheme is the remarkable **S** course taken by the inner of the two cubitals, but the grave disturbances are due to the excessive development of the two sub-costals. This leads to a somewhat similar condition to that seen in the wing-sac illustrated by fig. 101A. Here, instead of the anals, it is the sub-costals that bring about the atrophy of the radial, and here, as before, the supplying of the loss falls on the medial, the outer of the two medials assuming a radial form and function.

From the foregoing examples it will be seen that all the principal tracheæ, except the radial, are liable to duplication; all except the cubital, to a certain amount of reduction. In only one case was anything approaching a duplication of the

radial found. This is illustrated by figs. 103A and B. The chief interest attaching to this example lies in its uniqueness.

Figs. 104 to 134 (Plates VIII-IX) illustrate a number of wings selected from insects of one nest series which show a wide range of diversities and abnormalities. For convenience the word "wing" will be used instead of "figure," and it will be understood that whilst the drawings essay to picture the actual arrangement as far as possible, they do not show the marked difference that actually exists between the rigid and the flexible ribs.

Wings 104, 105, 108, 109, 112, 114 are all normal. Wings 107, 110, 111 are normal, but illustrate the occasional and more or less simple furcation of the media.

Wing 106, otherwise normal, possesses a remarkably well-branched media.

Wing 115 illustrates a unique case in which the media is drawn close to the radius.

Wing 116, whilst apparently but a more exaggerated illustration of an amply branched media, as in wing 106, more probably owes its condition to a duplicated medial.

The condition of wing 117 can be safely traced to a duplicated medial trachea. This wing is remarkable for the sharp and deep incurving of the tips of both media, the pre-existing tracheæ in this case, probably turning back as decidedly as tracheæ do in the wing-sacs of *Cryptotermes*, a feature that is further illustrated by wing 126.

Wing 121 is a hind wing in which the media is attached to the cubitus instead of to the radius, and this unusual state of affairs is accompanied by a short extra rib which occupies the place where the media would normally stand. Such a rib may arise from any one of several tracheal conditions. It might be due (a) to an extra but atrophied medial; (b) to a branch of the radial, as in fig. 103A (Pl. VII); (c) to a duplication of either the post-costal or the sub-costal, as in figs. 100 and 102A.

Wing 122: this abnormality can readily be traced to a duplicated medial, as in fig. 98A, the two tracheæ becoming

so closely applied to each other at half the wing-length that but one rib formed. Wing 123 equally owes its abnormal condition to a duplicated medial, both medials being atrophied and the tips of both touching the radial. The venation here illustrates the extra development of the cubital to make good the atrophy of the medial. Wing 124 owes its condition to a duplicated cubital, as in fig. 99A.

Wing 125 possesses a remarkable venation which does not give any very direct clue to the pre-existing tracheal tangle. It seems to me, however, to be due, in the first place, to a duplicated cubital, and, in the second place, to the crossing of the medial trachea by the outer cubital, so that the latter ran in between the medial and radial.

Wing 128 serves to illustrate the result following the crossing of principal tracheæ. Here it would seem that the medial was in duplicate, and the two stems crossed, somewhat as they do in fig. 97 (Pl. VII), the lower being briefly applied to the cubital. Wing 129 is one which conforms to the generic character for *Cryptotermes*, the media "joining the radius at about half the length of the wing." This is a case of the tip of a weak medial becoming applied to the radial.

Wing 131 suggests a duplicated medial in company with a duplicated cubital, the outer cubital being approximated to the medials. Wing 133 exhibits a duplication of the medial with the two tracheæ more or less atrophied and with the tip of each applied to the radial, the base of one associating itself with the radial and of the other with the cubital.

Wing 134 is a further illustration of a duplicated medial.

IXc. *CRYPTOTERMES* *sp.*

Plates IX and X, figs. 135A-154.

Except that in ninety-nine of every hundred wings of this species the media is found united to the radius at or about half the length of the wing, the structure of the wing-stumps, figs. 135A and 135B (Pl. IX), and the relationships of the

principal ribs are similar to those of *Calotermes*. That the generic character is not constant may be gathered from figs. 148 and 150 (Pl. X); it is true both the wings illustrated have an extra principal rib, but a normal wing has been found in which the media extended to the apex. Many wings are to be found in which the media possesses a strong branch or sector to the apex, such as those illustrated by figs. 143, 146 (Pl. X). This is seemingly the case in fig. 149, but here the condition appears due to the intrusion of an extra principal trachea into the wing-sac.

Cryptotermes wings differ strikingly from those of *Hodotermes* and *Calotermes* in the complete absence of reticulation. In many wings there are no ridges whatever; in others, again, there are curiously curved and erratically arranged ribs or cross-ribs exterior to the cubitus in the apical quarter, and these sometimes occur between the media and radius as in fig. 143. Where the media has no branch, the cubitus tends to invade its field, figs. 144, 147. "Independent" ribs are not uncommon; and they may appear actually independent as in fig. 152 or can be seen to be incurvings of the cubitus offsets as in figs. 146, 149.

Abnormalities due to the presence of extra principal tracheæ in the wing-sacs are to be met with, but not so frequently as in *Calotermes*. Such as have been found are traceable to a duplication of either the medial or the cubital trachea. Figs. 148, 149, 151 illustrate wings which seem to owe the unusual arrangement of the ribs to a duplicated cubital, whereas fig. 150 represents a duplication of the medial. In neither *Hodotermes* nor *Calotermes* was a hind wing found in which the pseudo-media or media did not attach itself more or less conspicuously to the radius; but one hind wing of *Cryptotermes*, fig. 152, shows the media attached to the cubitus.

The development of the tracheæ of the wing-sac has been dealt with elsewhere, and is similar to that of *Calotermes*, except there is no secondary development of many fibril-like tracheæ. A few do develop and are the predecessors of

the small cross-ribs already alluded to. The main tracheæ and their offsets do, however, lengthen considerably. Often the terminals of the radial, medial, and cubital travel for a considerable distance around the margin, and a remarkable extension of the cubital tip is shown in fig. 142 (Pl. IX). This wing-sac also illustrates the almost regular habit of the cubital offsets to dichotomise and for the branches to intermingle or turn back into the wing-sac.

The basal arrangement of the tracheæ is similar to that of *Calotermes*. This is shown, as seen in a preparation, by fig. 140 (Pl. IX).

In both fore and hind wing-sacs the post-costal and anal are present. In the younger nymphs the tracheæ first penetrate and develop in the wing-sac in more or less straight and parallel courses. In fig. 136 (Pl. IX) only the radial, medial, and cubital have developed. Two later stages are represented in figs. 137 and 138; both illustrate the late development of the anal. The radial and cubital branch about the same time; and, after this takes place, the tip of the medial inclines towards that of the radial, fig. 138; as the wing-sac grows, they extend, closely applied to each other, to and around its apex. When applied to the radial the medial is usually the more tenuous of the two. It may run quite evenly with it, fig. 139A; or entwine it, fig. 139B; or leave it abruptly, fig. 139C; or produce a straight or sinuous offset, figs. 139D and E; or an atrophied offset, fig. 139F. Sometimes the medial or its main offset bears one or several very fine branches, fig. 139G.

Further, after meeting the radial the growth of the medial may stop, or vice versâ, the radial may grow no further. In this event the medial assumes the function of the radial, simulating it by sending a series of branches to the outer margin. Abnormal schemes of tracheation were not met with in the long series of wing-sacs studied, other than the peculiar development of a trachea from the radial root shown in fig. 153 (Pl. X). The most unusual scheme was that reproduced by fig. 154.

IXd. RHINOTERMES PUTORIUS *Sjöstedt*.

Plate X, figs. 155-166.

The following notes are based upon too few wings and wing-sacs to be at all conclusive. As far as the observations go, they are, however, sufficiently interesting and important to include.

The *Rhinotermes* wing has much in common with the *Metatermite* type, more especially the more generalised as represented by *Termes* and *Odontotermes*. The principal differences lie in the absence of any trace of the sub-costa and in the greater area of the stump of the fore wing. As in the *Metatermite* wing the outer margin is supported by a pair of equally rigid, closely set, simple, and parallel ribs, and the remainder of the wing field by two principal flexible ribs. As compared with the wings of *Hodotermes*, *Calotermes*, *Cryptotermes*, the outer field is remarkably reduced. The two outer ribs are the costa and radius, and although no auxiliaries lie between them in the lamina, and the radius sends no branches to the costa, the two are connected by a number of struts, each forming a narrow isthmus and all arranged like the rungs of a ladder, figs. 155, 156 (Pl. X). The two remaining ribs I recognise as the pseudo-media and cubitus. In the fore wing these two fuse at the line of fracture, but within the wing-stump they are separated by a conspicuous fusiform space, fig. 157 (Pl. X). In the hind wing, the pseudo-media is attached to the radius just outside the line of fracture, and in this wing there is a marginal anal so atrophied as to be almost negligible, fig. 158.

The pseudo-media is more amply branched than in *Hodotermes*; and, as the radius has no inner (or sector) branches, it extends to the apex of the wing. Because it partakes of the nature of the cubitus it is well branched and the offsets of these two ribs support the inner wing-margin.

In figs. 157, 158 it will be noticed that in the wing-stump the costa is divided; the lower branch is the post-costa.

The foregoing interpretation is based upon an examination of the tracheæ of the wing-sac. Some young nymphs, with eight or nine months of development still before them, exhibited peculiar and somewhat erratic buds of wing tracheæ, and figs. 160 to 163 illustrate the conditions found in one of them. Fig. 160 shows the post-costa, radial, and furcate cubital; also a vestigial sub-costal on the radial. Fig. 161, although belonging to the mesonotum, is very different; here a similar post-costal is set much nearer a radial that wants the vestigial sub-costal, and against the stem of the furcate cubital springs a strong bud which may be considered as that of the medial. Fig. 162 is a condition analogous to that shown in fig. 161; the post-costal is, however, well removed from the radial and a medial springs from the stock of the cubital. Fig. 163 represents a fourth and very different condition; here the post-costal is as in the other wing-sacs, whilst, apparently, the radial and medial both spring from the stock of the cubital. Just what the subsequent development might be it is impossible to say, but in twenty-three out of twenty-four wing-sacs from six older nymphs, wanting a month or two for maturity, the condition of the tracheæ was as shown in fig. 164, except that in some the furcation of the cubital was much deeper-seated, so that the stock appeared to be double-barrelled. The tracheæ in the wing-sacs of these older nymphs probably had not reached their full development. It is to be noticed that the post-costal is fairly short and that the radial has similar branches to the radial of *Hodotermes*, *Calotermes*, and *Cryptotermes*; these branches need not, however, be regarded as the predecessors of the struts connecting the radius and costa in the final wing.

The one wing-sac that was unusual presented an extra trachea, fig. 165 (Pl. X), which may be regarded as the medial. An examination of the basal connections showed that this extra trachea arose from the cubital stem, fig. 166, a condition that might well be expected from the juvenile conditions already described.

I have found no final wing with an extra rib, but, curiously

enough, the reproduction of a photograph of the wings of this species (fig. 5, Pl. VI, Holmgren's 'Termitenstudien,' II) shows such an extra very clearly.

One feature of the *Rhinotermes* wing which the tracheæ, as studied, do not throw any light upon, is the marked extent to which it is ridged. This is so much the case that some ribs are not readily differentiated from the ridges. However, those between the offsets of the cubitus probably arise as they do in *Calotermes*, and the numerous oblique ridges between pseudo-media and radius may arise from tracheal branchlets of the former that had not developed in the wing-sacs studied.

IXe. PSAMMOTERMES ALLOCERUS *Silv.*

Plate X, figs. 167-173.

In *Rhinotermes* it has been shown that the medial trachea and therefore the media is normally wanting; there is some evidence to show that it may be occasionally present. This is also the case in *Psammotermes*, and later it will be shown that in *Termes natalensis* an extended examination of wing-sacs and wings has failed to show any trace of a medial. Upon the other hand, the medial (and media) is regularly present with *Calotermes* and *Cryptotermes*, and although it tends towards decadency in the latter there is ample evidence of what may be described as an effort to re-establish itself as one of the principals. The conclusion one comes to is that in certain generalised termites the medial has become suppressed by the regular and strong development of a duplicated cubital. In *Calotermes* and *Cryptotermes* it has been seen that any deviation of the medial from its field or any atrophy that occurs is made good by the cubital. In short, the cubital seems ever ready to assume the chief aerating route of the wing-sac.

The following remarks upon the wings of *Psammotermes* are introduced only to illustrate the aggressiveness of the cubital. They are based upon the examination of twenty

laminae and have little other interest, as no wing-sacs of the nymphs of this species have been available for study. It is thought, however, that the tracheation is analogous to that of *Rhinotermes* except that the cubital is not regularly duplicated.

The outer field of the wing—as apart from the stump—is supported by two simple parallel chitinised ribs; these are the costa and radius. There is no trace of an intervening auxiliary or of connecting supports such as are found in *Rhinotermes* and *Termes*. Both costa and radius are, whilst rigid, quite slender, and the latter tapers off before the former. The wings examined fall into two groups, those in which a median rib is present, and those in which there is no trace of such. This rib I take to be the media because of its simplicity. When present in the fore wing, fig. 167 (Pl. X), it is fused to the cubitus, and, when present in the hind wing, to the radius, fig. 168. Of the twenty wings examined, such a media was present in seven; of these, two were fore wings and the rest hind wings. In the remainder the cubitus was highly developed, the degree varying as between figs. 169 to 173. In the hind wing there is present a very inconspicuous anal. It is possible that in some of the wings the cubital trachea was duplicated, but this is pure speculation.

IXf. *TERMES NATALENSIS* *Haviland*.

Plate XI, figs. 174–179.

As between the wings of *T. natalensis* (with its races and such local allies as *T. bellicosus*, *T. swaziæ*, and *T. waterbergi*) and those of *Rhinotermes putorius* there is a general likeness of structure, particularly as regards the nature and arrangement of the two principal ribs, pseudo-media and cubitus. Especially is this the case within the laminae. Here, however, there are a number of differences, some more important than others. The laminae agree inso-much that the outer margin is supported by a pair of close-set parallel ribs of equal strength and rigidity, the costa and

radius. They also agree in that the membrane derives its main support from a pseudo-media and cubitus. The principal point of difference is that, inset between the bases of the two outer ribs, there is a short auxiliary, the rudiment of a subcosta. Other differences that may be cited are: (a) the absence of an anal from the hind wing; (b) of struts between radius and costa (occasionally one such strut is to be found in the wings of *T. swaziæ*); (c) the obliterated condition of the "reticulation"; (d) the frequent presence of inner branches (sectors) to the radius. The general features of the *Termes* wing are illustrated in figs. 174, 175 (Pl. XI); but in these no attempt has been made to indicate the obliterated reticulation to which reference has been made, and both wings exhibit sectors to the radius.

Considerably over 100 wings of one nest series, together with a number of minor lots, were searched without avail for abnormalities of venation, and this is remarkable inasmuch that the tracheation of the wing-sac is so extensive and in some particular features curiously variable. The full development of the tracheæ is traced in fig. 176 (Pl. XI) and parts of the scheme are drawn upon a larger scale in figs. 177 and 178. As in *Hodotermes* and *Rhinotermes* this tracheal display originates in the main from two roots or basal connections, the radial and cubital. Figs. 179 and 180 are sketches showing the genesis of wing tracheæ, 179 of the meso- and 180 of the metathorax. Here the normal condition appears reversed, a greater development having taken place on the cardinal of the metathorax. That this is unusual may be seen from fig. 181, wherein not only is the mesothoracic wing-sac the larger but the post-costal is present, whereas it has not yet put in an appearance in the metathoracic sac. In this particular instance the post-costal is in the position that is normal for *Hodotermes*, *Calotermes*, and *Cryptotermes*. The second development is that of a sub-costal, and later the anal may appear. The only principal trachea that is ever absent is the last mentioned, as in figs. 183 and 185. It may be present in an atrophied condition, fig. 184,

but is generally well-developed, figs. 182, 187; as a rule it arises from the cubital, but has been found occupying an independent position on the cardinal as shown in fig. 187. In all cases, when present, the anal trachea is directed away from the wing-sac into the thoracic cavity. The basal attachment of the post-costal is most erratic. It may spring from the radial, figs. 184, 185; it may be independent (as in *Rhinotermes*), fig. 182, but more often it arises from the stock of an arborescent bunch of tracheæ anterior to the union of the cephalic arm of the leg-trachea with the cardinal, figs. 183, 186, 187. The radial usually stands independent upon the cardinal, but has twice been found close to, fig. 185, or arising from, fig. 183, the stock of the cubital. In but one nymph has anything approaching the development of a medial trachea been observed, fig. 187. In any one nymph of *T. natalensis* four differing conditions may be found as regards the basal connections of the tracheæ of the four wing-sacs.

With reference to the post-costal trachea it may be added that it is readily observed lying within the large outer shoulder-like ridge of the wing-stump of the adult, should the insect be fresh and not too long fledged.

IXg. *MICROTERMES INCERTUS* (*Hav.*).

Plate XI, figs. 188-200.

The wings of this insect have the same structure as those of *Termes natalensis*, etc., but display less regularity. The main point of difference is that there is no inner branch to the radius in ninety-eight out of every hundred wings. Compare fig. 190 with others. Occasionally, the radius and costa are linked together by small struts, reminding one of those common to the *Rhinotermes* wing, but each is obviously an isthmus arising during chitinisation, figs. 188, 189, 193. The irregularity that is most noticeable is due to the rare presence of a true media, figs. 191, 192 (Pl. XI), and to the occasional union of this with the radius, figs. 192, 193. However, considering the frequency with which a medial trachea is

present in wing-sacs, it is remarkable that more evidence of it is not to be found in final wings. It is possible, however, that the thickening forming about it coalesces with that forming about the pseudo-medial, and any branches it may produce appear in the final wing as branches of the pseudo-media.

From an examination of a considerable number of nymphs in various stages of growth, it is possible to say that ordinarily the tracheæ of the wing-sac arise from two buds, the radial and the cubital, of which the latter is the first to develop; compare figs. 195, 196 with fig. 197. In a later stage the three principals are found as in fig. 198. Still later, developments comprise, ordinarily, the branching of the cubital and the appearance of a sub-costal. Extraordinarily, a post-costal or an anal, or both, may appear, fig. 199, and either of these two tracheæ may lie extended into the wing-sac or may bend back into the thoracic cavity.

Quite frequently the wing-sac is penetrated by a principal trachea, extra to the normal quota; this is the medial, fig. 200. In all cases except one, in which such a medial was found, the cubital was duplicated. In the one exception the cubital was single, but the medial was duplicated.

Concerning the wings reproduced it may be said that figs. 188, 189 represent companion fore and hind wings, both of which may be considered as normal, but the condition of the hind wing, fig. 189, gives rise to the suspicion that the venation is due to a true media as well as a pseudo-media and cubitus. Fig. 190 represents a normal wing; the only one noticed in which the radius possessed a true inner branch or sector. Fig. 191 is a wing in which the media is undoubtedly fully developed, and in the two wings, figs. 192, 193, I think the rib which unites with the radius arises from a true medial trachea. Fig. 194 represents a quite abnormal condition due to the pseudo-medial trachea applying itself in part to the radial.

IVh. MISCELLANEOUS SPECIES.

Plate XI, figs. 201-207.

Odontotermes.

It has been ascertained that the chief tracheæ of the wing-sac in *O. badius* and *O. latericius*, fig. 55 (Pl. VI), are the radial, pseudo-medial, and cubital, as in *T. natalensis*.

Microtermes sp.

A *Microtermes*, related to *M. albopartitus* (*Sjostedt*) found near Pretoria, displays three principal tracheæ, a radial, a medial, and a cubital; the radial bearing a reduced subcostal. In all the specimens examined the basal attachment of the cubital was far removed from that of the medial and that of the medial well separated from the base of the radial. In this respect and inasmuch as the cubital was not found duplicated, this species differs from *M. incertus*. In one wing-sac, however, the base of the radial stood against that of the medial; this is illustrated by fig. 205 (Pl. XI), a figure which also shows the remarkable loops made by the tracheæ to enter the wing-sac of the more mature nymphs.

Eutermes (*trinervius* group).

Numerous studies show that the chief tracheæ of the wing-sac of two or three species are regularly the radial, medial, and cubital. In no case was the cubital or any other found in a duplicated condition. The base of the cubital is always far distant from that of the medial, figs. 203, 204 (Pl. XI). When the nymphs are but moderately grown the three tracheæ stand in the relationship to one another seen in fig. 203; but, later, the cubital and medial are closely applied as they enter the wing-sac, fig. 204. Many wings have been searched for extra principal ribs, but only two were found. In one wing there were two median ribs, the outer simple and running straight to the wing apex, the inner also extending to the wing apex but sending three offsets to the inner margin of the wing. In the other wing, fig. 202, there were

also two median ribs, the two being united for a short distance at half the length of the wing; the companion of this wing, fig. 201, presented a normal venation.

Cubitermes bilobatus (*Hav.*).

The chief tracheæ are as in *Eutermes* (*trinervius* group). In one case, figs. 206A, B (Pl. XI), a vestigial post-costal was found.

Hamitermes hastatus (*Hav.*).

The chief tracheæ are as with *Eutermes* (*trinervius* group). Fig. 207 (Pl. XI) is a sketch from a preparation showing some of the late tracheal developments that occur about the region of the spiracles.

Promirotermes.

Several immature nymphs of two species have been examined and show a radial, medial, and cubital. In one wing-sac there appeared to be a duplication of the medial, fig. 208 (Pl. XI), but it was not possible to trace the basal connections.

APPENDIX.

LIST OF SPECIES REFERRED TO IN TEXT.

The localities given are those from which the material examined was obtained.

- (1) *Hodotermes viator* *Latreille*.

Cape Province: Springbok (Klein Namaqualand).

- (2) *Hodotermes karrooensis* *Fuller*.

Cape Province: Victoria West, Middelburg.

- (3) *Hodotermes transvaalensis* *Fuller*.

Transvaal: Pretoria.

- (4) *Calotermes durbanensis* *Haviland*.

Natal: Durban, Winklespruit, Illovo River.

Remarks: In 1898 Haviland described this insect

from specimens of soldiers and workers obtained by James Wylie from trees in the Botanic Gardens, Durban. Some of the nymphs and winged imagos, as well as soldiers and workers which I examined were from the same trees or near-by sources. There is no doubt whatever that the insect to which I have applied Haviland's name is the species he described. It abounds along the seaboard of Natal from the scrub of the beach to well inland.

Sjostedt, who compared Haviland's types with those of *Calotermes madagascarensis* Wasman (1900), placed *C. durbanensis* as a synonym of Wasman's species. Desneux follows Sjostedt. Holmgren does not mention *C. durbanensis* in his list of African species. However, he places *C. madagascarensis* in his sub-genus *Proneotermes* and places only American species in his *Calotermes sensu stricto*. It will be obvious from the description of the soldiers which I have given elsewhere¹ and from the wing-studies here presented that the insect can only be placed as a *Calotermes* *sen. str.*, and, therefore, it can only be discussed as *Calotermes durbanensis* *Haviland*.

(5) *Cryptotermes* sp.

Natal: Durban, Winklespruit, Illovo River.

Remarks: Imago resembling *C. havilandi* (*Sjost.*), soldier differing from *C. havilandi* (*Sjost.*), as described by Silvestri.

(6) *Rhinotermes putorius* *Sjost.*

Natal: Durban. Moçambique: Busi River.

(7) *Psammotermes allocerus* *Silvestri*.

Ovamboland: Namukunde. Cape Province: Van Rhynsdorp, Springbok, Steinkop.

¹ 'Ann. Nat. Mus.', p. 451, vol. iii, part 2, 1915.

- (8) *Termes bellicosus Smeathman*.
Transvaal: Limpopo River. Moçambique: Busi River.
- (9) *Termes natalensis Haviland*.
Transvaal: Pretoria. Natal: Hillcrest.
- (10) *Odontotermes badius (Haviland)*.
Transvaal: Pretoria.
- (11) *Odontotermes latericius (Haviland)*.
Transvaal: Pretoria.
- (12) *Microtermes incertus (Haviland)*.
Transvaal: Pretoria.
- (13) *Microtermes* sp. (near *M. albopartitus Sjostedt*).
Transvaal: Pienaar's River.
- (14) *Eutermes* spp. (*trinervius* group).
Transvaal: Pretoria, Pienaar's River.
- (15) *Cubitermes bilobatus (Hav.)*.
Transvaal: Pretoria.
- (16) *Hamitermes hastatus (Haviland)*.
Cape Province: Port Elizabeth.
Hamitermes hastatus (Hav.), var. *capicola Silvestri*.
Transvaal: Pretoria.
- (17) *Promicrotermes* sp.
Natal: Ixopo.
- (18) *Microcerotermes* spp.
Microcerotermes sp., near *M. parvus (Haviland)*.
Transvaal: Pretoria.
Microcerotermes sp., near *M. zuluensis Holmgren*.
Transvaal: Pretoria. Natal: Durban.
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EXPLANATION OF PLATES III—XI,

Illustrating Mr. Claude Fuller's paper, "The Wing Venation and Respiratory System of Certain South African Termites."

PLATE III.

FIG. 1.—Wing venation : Comstock and Needham's hypothetical type.

FIG. 2.—Hypothetical primitive element of respiratory system ; *sp.*, spiracle ; *tr.*, tracheal pipe, and its three primary subdivisions : *a*, ascending ; *b*, horizontal ; *c*, descending trachea.

FIG. 3.—Hypothetical development of ascending trachea (*a* of fig. 2) ; *aa. aa.*, branches which go to form the dorsal longitudinal trunk.

FIG. 4.—Spiracles VIII, IX, X, with *a.a.a.*, palisade commissures ; *Dl. t.*, dorsal longitudinal trunk and its cauda. The visceral tracheæ are omitted. (Diagram.)

FIG. 5.—Hypothetical development of descending tracheæ (*c* of fig. 2) from opposite spiracles, so as to meet and form a ventral commissure.

FIG. 6.—Hypothetical development of horizontal trachea (*b* of fig. 2), so as to link up the spiracles and form the spiracular trunk.

FIG. 7.—Spiracles VIII, IX, X, with the horizontal tracheæ united to the descending trachea of each anterior spiracle, illustrating the indirect primary air route from spiracle to spiracle. (Diagram.)

FIG. 8.—A transverse section of the system.

FIG. 9.—Side view of the system, including spiracles II and III, showing the attachment of the Y-shaped trachea of the second and third legs to the spiracular trunk (*Sp. t.*), and, at *x.x.*, the separation of the tracheæ in the region of the tibiæ.

FIG. 10.—Section of the system about spiracles X (the last abdominal), illustrating the paired visceral tracheæ (*x.x.*) from which the palisade commissures seem to arise.

FIG. 11.—Dorsal and lateral parts of the body system, showing the paired dorsal longitudinal trunks, the paired spiracular trunks, the two sets of palisade commissures, and, *x.x.x.x.*, the series of buds upon the dorsal longitudinal trunks.

FIG. 12.—The dorsal longitudinal trunks with the arborescent tracheæ which develop from the buds (*x.x.x.x.* of fig. 11) and which pervade the dome of the body.

FIG. 13.—Ventral parts of the body system, showing the spiracular trunks, the leg tracheæ, and, in solid black, the ten ventral commissures and the cervical commissure which links up the tracheæ of the first pair of legs.

FIG. 14.—The great U-shaped trachea of the head (including spiracles I) with the bases of the tracheæ attached to it; *ll.*, of first legs; *m.m.*, of mouth parts; *x.x.*, of the great dorsal tracheæ; *z.z.*, of commissures to dorsal tracheæ. (Diagram.)

FIG. 15.—The frame of the tracheal system of the head, including spiracles I, and showing the U-shaped tracheæ; *x.x.*, the paired dorsals terminating at *y.y.* in the tips of the antennæ; and *z.z.*, the vertical commissures. (Diagram.)

FIG. 16.—The tracheæ of the first pair of legs, including spiracles I and showing *c.c.*, the cervical commissure.

FIG. 17.—The upper region of the respiratory system of the head including a part of the U-shaped trachea; *a.a.*, the tracheæ of the dorso-lateral extensions of the prothorax; *b.b.*, the connections of the dorsal longitudinal trunks with the great dorsal tracheæ of the head; *c.c.*, the tracheæ of the genæ; *d.d.*, the tracheæ of the vertex; *e.e.*, the complex of the frons. (Diagram.)

FIGS. 18 and 19 show the tracheal system of the head, and were designed from a series of camera lucida sketches of cleared preparations of the newly-hatched young of *Odontotermes latericius*. The various tracheæ may be recognised by comparison of these figures with figs. 14, 15, 17.

FIG. 18.—From below, the nearer or more ventral tracheæ are shown in solid black, the further or more dorsal are shaded. The parts and organs of the head are faintly outlined.

FIG. 19.—From the side (partly from below), showing, in chief, the nearer half of the system; also, the tracheæ of the first legs, part of the first ventral commissure, the Y-shaped tracheæ of the nearer mesothoracic leg, a part of the dorsal longitudinal trunk, and the first palisade trachea of the thorax.

PLATE IV.

FIG. 20A.—Diagrammatic representations of the tracheal system as seen in the newly-hatched young of *T. natalensis*, *Odontotermes latericius*, and *Microtermes incertus*. On the left, as looked through from above; on the right, as seen when the dorsal longitudinal trunk is thrown aside.

FIG. 20B.—The main system as seen from the side in the cleared preparation of the newly-hatched young of *T. natalensis*.

FIG. 21A.—The system of the newly-hatched young of *Cryptotermes* as seen from below. It illustrates the early arrangement of the ventral longitudinal trunks linking up the ventral commissures; the anastomosis of the cervical with the first ventral commissure; the commissure linking up the two ventral trunk tracheæ of the head; the tracheæ of the mouth-parts. (The routes of the paired tracheæ of the labrum are indicated by dotted lines. The palisade commissures and the dorsal longitudinal trunks being the same as those in the metatermite stem, are omitted).

FIG. 21B.—The dorsal tracheæ of the head of *Cryptotermes*, as arranged in the second stage of their development. (The tracheæ of the vertex and genæ are shown in solid black).

FIG. 21C.—The dorsal tracheæ of the head of *Cryptotermes*, as seen in the newly-hatched young.

Inset: The mandibles of the nymph of *Eutermes* *sp.*, showing how both are composed of three well-defined regions.

PLATE V.

FIGS. 22A to 22H.—These figures show the development of the pipes of the thoracic spiracles from enlarged tubes to air-sacs, figs. 22A to 22E being of the first pair, and figs. 22F, G, H of the second pair. All are proportionately enlarged except fig. 22E, which is drawn upon a smaller scale. The conditions represented by figs. 22F and G accompany the conditions of the first spiracle in figs. 22A to D; fig. 22H of the second spiracle accompanies the condition seen in fig. 22E of the first spiracle. All figures are from camera lucida sketches of nymphs of *Microtermes incertus*. The bases of the tracheæ shown are in figs. 22A to 22E those of: (1) The dorsal trachea of the head which terminates in the tip of the antenna; (2) the stem of the U-shaped ventral trachea of the head which bears the tracheæ of the mouth-parts; (3) the trachea of the first leg; (4) the ventral commissure of spiracles I; (5) the trachea to the second spiracle. In figs. 22F, G, H they are the bases of (1) the trachea to the first spiracle; (1a) the trachea to the third (or first abdominal) spiracle; (3) the ventral commissure of spiracles II.

FIGS. 23A, B, C.—These figures illustrate the apparent arrangement of the abdominal series of spiracles (spiracles III to X as seen from within) in the newly-hatched young of *T. natalensis* and *T. latericius*. The features shown are: (1) The circular pore or fixed opening in the cuticle; (2) the atrium; (2a) the vestigial resister; (3) the lever; (4) the epitrachelos; (5) the trachelos; (6) the tracheal pipe; (*oc. m.*) the oclucor; (*ex. m.*) the extensor muscle.

Figs. 23A and B show the spiracle open and 23C closed. In 23B the

epitrachelos is removed to show (in solid black) the side opening in the organ through which the air passes into the epitrachelos. In 23c the epitrachelos is seen closed by the pinching of the lever against the resister (more or less diagrammatic).

FIGS. 24A and 24B.—The abdominal spiracle in the second stage of development (*T. natalensis*). Fig. 24A, viewed from within; fig. 24B, the outer aspect. Both figures illustrate the development of the resister and its hiatus, the extension of the trachelos, and the disappearance of the epitrachelos.

FIGS. 25A, B, C.—Sections of the lever, showing the hypothetical development or change from an ascidium to a plate. (Diagrams.)

FIG. 26A.—A section of the base of the atrium, showing how, in the second stage spiracle, the resister protrudes into the lumen. (Diagram.)

FIG. 26B.—An interior view of the resister, showing the hiatus and bulge. (Diagram.)

FIGS. 27A and B.—The resister and lever, showing dorsal strap or fulcrum connecting the two; fig. 27A, viewed from within; fig. 27B, the outer aspect. (Diagrams.)

FIGS. 28A and B.—The resister and lever with muscle attached; fig. 28A, attitude when the lumen is open; fig. 28B, when the lumen is closed. (Diagrams.)

FIGS. 29A and B.—Dorsal aspect of spiracles; fig. 29A, showing the lever drawn against the resister and the lumen closed; fig. 29B, showing the relationship of lever to resister when the lumen is open. (Diagrams.)

FIG. 30.—Abdominal spiracle in transition between second and third stages (*T. natalensis*). View from within, showing *nr.*, a new rim developing behind the rim of the pore (*pr.*), and *ch.*, the large chin-plate that develops on the side of the atrium against the resister.

FIGS. 31A, B, C.—Abdominal spiracle of the third stage (*T. natalensis*). Fig. 31A, viewed from within, showing (1) the shortening of the atrium; (2) the tympanic chin-plate; (3) the compressed resister; (4) the hexagonal, tessellated trachelos pinched against the resister by (5) the lever. The position of the lever, when open, is also indicated. Fig. 31B, outer aspect; a diagram representing the throwing off of the pore and atrium, or the transition of the spiracle from the third to fourth stage. (Compare the left-hand part of the diagram with fig. 34.) Fig. 31C, diagram representing the same, but viewed from above.

FIG. 32.—Spiracle III (the first abdominal) of *T. natalensis*, female. External aspect viewed from the side, illustrating a distinct transformation to the bivalvular form in which *R.* the resister is

reduced to form a narrow edge to *C.*, the tympanic chin-plate, and *L.*, the lever has developed a strong thumb-like projection. The trachelos (*m. tr.*) is also seen within the open mouth of the spiracle. (The cuticle is not indicated.)

FIG. 33.—Spiracle IV (the second abdominal) of *T. natalensis*, female: not so decidedly transformed as spiracle III. Lettering as for fig. 32.

FIG. 34.—Spiracle X (the last abdominal) of *T. natalensis*, female; still less decidedly transformed. Lettering as for fig. 32.

FIG. 35.—Abdominal spiracle of *Hodotermes*, female, as seen from the outside, showing the two thumb-like projections to which the muscles are attached. Lettering as for fig. 32.

FIGS. 36A, B, C.—The abdominal spiracles of *Hodotermes*, male, fig. 36A, from without; fig. 36B, from within, open; fig. 36C, from within, closed.

FIG. 37.—The rim (from within) of the spiracle of the second stage, *T. natalensis* (fig. 24A), showing the hexagonal (tessellated) framework.

FIGS. 38A, B, C.—The thoracic spiracles of *T. swaziæ*, fig. 38A, the second; fig. 38B, the first; fig. 38C, the second disrupted to separate the occlusor from the extensor muscle drawn on a much smaller scale than 38A.

FIG. 39.—The tracheæ of the femur in the half-grown nymph of *T. natalensis*.

FIGS. 40, 41, 42, 43A and 43B, progressive stages in the development of the abdominal pipes of the female nymph of *T. natalensis*. Fig. 40, the distension of the pipes; figs. 41 and 42, two stages of the growth of the multitude of dichotomising tracheæ from the pipes; fig. 41, *p. com.*, palisade commissure; *d. tr.*, dorsal trunk; *v. com.*, ventral commissure; *sp. tr.*, spiracular trunk. Fig. 43A, an outer aspect of the tracheal arrangement about the abdominal spiracles of an almost mature nymph, showing *sp. tr.*, the spiracular trunk; *vc. vc.*, ventral commissures; *pc. pc.*, palisade commissures; *O. C.*, the ovarian chord embraced by two of the tracheal bunches. Fig. 43B, the inner aspect of the arrangement represented by fig. 43A, showing two perpendicular and one oblique muscle and the peristaltic ribbon.

FIG. 44.—A side view of an abdominal spiracle of the adult female (*T. natalensis*), showing *L.*, the lever; *trl.*, the trachelos, and some of the many dichotomising tracheæ that open into the cup formed by the trachelos.

FIG. 45A.—A part of a disrupted spiracle of the distended female (queen) of *Odontotermes badius*, showing how the tracheæ open freely into the disruption.

FIG. 45B.—Outside aspect of the disrupted spiracle of the distended female of *T. natalensis*, showing the mouths of the tracheæ and the tracheate character of the disruption.

FIG. 46.—Diagram of the tracheal stem (Metatermite) of the head and thorax.

FIG. 47.—Diagram of the tracheal stem (Metatermite) to illustrate homologies.

FIG. 48.—Diagram of a section of the tracheal stem of the Calotermite type, to show that the wing tracheæ originate from the spiracular trunk; both the dorsal longitudinal and the ventral longitudinal tracheæ being present.

PLATE VI.

FIG. 49.—Thorax of a young *Cryptotermes* nymph, illustrating the lateral bulging out of the spiracular trunk (shown in solid black) within the meso- and metathorax.

FIGS. 50A, B, C.—The genesis of a trachea bud in three stages of development; as found on a series of tracheal pipes in the abdomen of a *Calotermes* nymph.

FIG. 51.—The buds of wing tracheæ.

FIG. 52.—Clavate tubercles of wing tracheæ.

FIG. 53.—Conical tubercles of wing tracheæ.

FIG. 54.—The sub-apical growth of tracheæ from tubercles.

FIG. 55.—Wing-sac of very young nymph of *Odontotermes latericius* with a simple conical bud (the radial) and a furcate bud (the cubital).

FIG. 56.—The bud of the post-costal (*Pst. c.*) on base of radial (*R.*). (*Cryptotermes.*)

FIG. 57.—The vermiform bud of sub-costal (*Sc.*) on radial. (*Cryptotermes.*)

FIG. 58.—Early form of anal (*A.*) on cubital (*Cu.*). (*Cryptotermes.*)

FIG. 59.—Fore and hind wing-sacs of *Cryptotermes*, showing the early form of the six principal tracheæ.

FIG. 60.—The lateral tracheæ of the thorax of *Cryptotermes*; *a.a.a.*, dorsal longitudinal; *b.f.b.*, spiracular trunk; *c.*, first spiracle of abdomen; *d.*, second spiracle of thorax; *e.e.*, arms of leg tracheæ; *g.*, stem of leg trachea.

FIG. 61.—Wing-sac of full-grown nymph (*T. natalensis*), illustrating the beginning of the growth and folding of the final wing, accompanied by the displacement and coiling up of the tracheæ. Tracheæ in focus

shown in solid black, those further away are shaded; the thickening of the margin is also indicated; *c.*, costal thickening; *R.*, radial; *Ps. M.*, pseudo-medial; *Cu.*, cubital.

FIGS. 62A and B.—These figures illustrate the migration of a trachea from the thickening that forms about it.

FIGS. 63A and B.—The figures illustrate the movement of the cubital offsets from thickenings and the forming of new bands about them in their new positions.

FIG. 64.—The wing of *T. natalensis* as it appears before and after the last ecdysis. Viewed from below.

FIGS. 65A to 65K.—The various stages of the unfolding of the wing of *T. natalensis* (side views; the diagrams are all of the same relative enlargement). Fig. 65A represents the condition shown in fig. 64; figs. 65B, C, D, E, the conditions seen in figs. 67A, B. Fig. 65K represents a fully expanded wing.

FIG. 66.—*T. natalensis*; imago with wings unfolding.

FIGS. 67A, B, C, D.—*T. natalensis*; wings in various stages of unfolding; A, B, C, from above; D, from below.

FIG. 68.—*Calotermes durbanensis*; basal half of freshly unfolded and transparent wing, showing the thickenings then present and (in solid black) the lumina; *x.*, the cross-rib, with lumen, connecting post-costa to costa.

FIG. 69.—Diagram representing the stretched-out condition of the spiral of the lumina of fig. 68.

FIGS. 70A and B.—*Hodotermes karrooensis*; fig. 70A, wing-stump and base of lamina of fore wing; fig. 70B, the same of hind wing.

FIG. 71.—*Hodotermes viator*; illustrating the abnormal position of pseudo-media (in solid black) in a particular hind wing.

FIGS. 72A and B.—*H. viator*; illustrating the abnormal duplication of the sub-costa (in solid black).

FIG. 73.—*H. viator*; illustrating the deep furcation of the sub-costa (in solid black).

FIG. 74.—*H. viator*; illustrating the deep furcation of the post-costa (in solid black).

FIG. 75.—*Hodotermes transvaalensis*; portion of wing-base illustrating the absence of a pseudo-media.

FIG. 76.—*H. transvaalensis*; illustrating the duplication of the pseudo-media (in solid black).

FIG. 77.—*Hodotermes viator*; illustrating an abnormally well-branched condition of the sub-costa (in solid black).

PLATE VII.

FIG. 78.—*Hodotermes viator*; wing-sac of nearly mature nymph with the detail of the tracheæ; *x.*, the trachea preceding the cross-rib from post-costa to costa. Post-costal independent.

FIG. 79.—*H. viator*; an abnormally reduced inner cubital (*Cu.*).

FIGS. 80, 81, 82, 83.—*H. viator*; the cardinal trachea and the basal connections of the tracheæ of the wing-sac, illustrating abnormal developments. Fig. 80 (? *M.* in solid black), an extra trachea, probably the medial, originating from the base of (*ps.-m.*) the outer cubital (or pseudo-medial). Fig. 81, a deeply furcate (or duplicated) post-costal (in solid black). Fig. 82, an extra principal trachea (in solid black) entering the wing-sac and associated with the radial. Fig. 83, the pseudo-medial, cubital, and anal arising almost independently.

FIGS. 84A, B, C, D.—*H. viator*, normal wings; fig. 84A, fore wing; figs. 84B, C, D, hind wings.

FIGS. 85 and 86.—*Calotermes durbanensis*; wing-stump and base of lamina; fig. 85, of fore wing; fig. 86, of hind wing.

FIG. 87.—*C. durbanensis*; part of lamina of hind wing with (in solid black) an independent post-costa.

FIGS. 88–103B represent the development and abnormalities of the tracheæ of the wing-sac of *C. durbanensis*. FIGS. 88–97, 101A and 102A are more or less in proportion.

FIGS. 88–94.—These illustrate the normal progressive development of the tracheæ, commencing from the hinder wing-sac of fig. 88. In fig. 88 the more advanced condition of the tracheæ of the meso-thoracic wing-sac (of a moderately young nymph) is well-marked. In fig. 91 the branch to the sub-costal is an unusual feature. In fig. 94 is shown that extension of the principals, and that growth from these of many small tracheæ, to be found in the wing-sac of a nymph, in the last stadium, prior to the development of the final wing.

FIG. 95.—An abnormal medial (in solid black); the trachea has two strong outer branches which cross one another and extend to the apex of the sac.

FIG. 96.—A medial (in solid black) taking an abnormal path in crossing the cubital, and extending to the inner margin of the sac.

FIG. 97.—An abnormal medial (in solid black) duplicated from the cardinal, the two tracheæ crossing.

FIGS. 98A and B.—Illustrating the basal connection of an extra principal trachea with the medial. In fig. 98A the extra trachea is shown in solid black; in fig. 98B the junction of the two is illustrated.

FIGS. 99A and B.—Illustrating the basal connection of an extra principal trachea with the cubital. In fig. 99A the extra trachea is shown in solid black; in fig. 99B the attachment of it and the anal to the cubital is illustrated.

FIG. 100.—Illustrating the basal arrangement of the tracheæ of a wing-sac in which the post-costal and cubital were found duplicated.

FIG. 101A.—A wing-sac in the same condition of development as that shown in fig. 94, with an abnormal scheme due to the displacement and extraordinary development of a furcate anal (in solid black). Other abnormal features are: (1) The absence of the sub-costal; (2) the reduced and branchless condition of the radial; (3) the branched condition and displacement of the medial; (4) the large outer branches of the cubital.

FIG. 101B.—The basal connection of the furcate anal of fig. 101A with the cubital is shown.

FIG. 102A.—Wing-sac in the same condition of development as that shown in fig. 94, with an abnormal scheme due to the presence of three extra principal trachea, the sub-costal, medial, and cubital all being duplicated.

FIG. 102B.—The basal connection of the duplicated sub-costal with the radial is shown.

FIGS. 103A and B.—These illustrate the unusual development of an inner branch upon the base of the radial. Fig. 103B shows the basal part of this unusual branch.

PLATE VIII.

Calotermes durbanensis.

Wings with normal and sub-normal venation.

FIG. 104.—Fore; normal; *M.* with furcate tip and no basal branches; *R.* with cross-branch to *Sc.*

FIG. 105.—Hind; normal; *M.* simple, with three short basal branches.

FIG. 106.—Hind; normal; *M.* unusually subdivided.

FIG. 107.—Fore; normal; *M.* somewhat deeply furcate, with many cross-branches between *M.* and *R.*; offsets of *R.* furcate.

FIG. 108.—Fore; normal; with *M.* faintly furcate and with two-hooked basal branches.

FIG. 109.—Hind; normal; *M.* simple, with three basal branches; *R.* with cross-branch to *Sc.*

FIG. 110.—Hind; normal; *M.* furcate without basal branches.

FIG. 111.—Hind; normal; *M.* furcate with two curved basal branches.

FIG. 112.—Hind; normal; *M.* with an uncinat basal branch.

FIG. 113.—Fore; sub-normal; *M.* and *Cu.* connected by a cross-branch; *M.* with sinuate basal branches (cf. fig. 119).

FIG. 114.—Fore; normal; *M.* simple with two long basal branches, forming cells.

Wings with sub-normal and abnormal venation.

FIG. 115.—Hind; abnormal; *M.* simple but approximated to *R.*

FIG. 116.—Hind; sub-normal; *M.* deeply furcate and subdivided.

FIG. 117.—Hind; abnormal; *M.* duplicated with both tips strongly incurved.

FIG. 118.—Fore; abnormal; *M.* and *Cu.* fused (probably due to crossing of tracheæ *M.* and *Cu.*).

FIG. 119.—Fore; sub-normal; *M.* and *Cu.* fused; ridges between cubitus offsets recording movement of pre-existing tracheæ. (Compare with fig. 113.)

FIG. 120.—Hind; abnormal; *M.* deeply furcate or duplicated; *M.* and *Cu.* connected by cross-branch (probably due to crossing of branches of trachea *M.* and to crossing of trachea *Cu.* by these branches).

FIG. 121.—Hind; abnormal.

FIG. 122.—Hind; abnormal; *M.* duplicated in basal half of wing.

FIG. 123.—Fore; abnormal; *Sc.* furcate; *M.* reduced and united to *R.* (probably due to a duplication of trachea *M.* accompanied by reduction); *Cu.* highly developed and connected to *R.* by cross-branches characteristic of *M.*

PLATE IX.

Calotermes durbanensis.

Wings with abnormal venation.

FIG. 124.—Fore; abnormal; probably owing to duplication of cubital trachea; *R.* with cross-branch to *Sc.*

FIG. 125.—Fore; very abnormal; condition not readily explained, but due to tracheal tangle.

FIG. 126.—Hind; abnormal on account of independents between cubitus offsets; *M.* subdivided at apex, with a long, bicurvate cross-branch to *R.* at base.

FIG. 127.—Fore; abnormal; *M.* furcate, crossing *Cu.*, with an uncinate branch at base.

FIG. 128.—Fore; abnormal; *M.* deeply furcate; condition due to crossing of tracheæ.

FIG. 129.—Hind; abnormal; *M.* reduced and fused to *R.*; *Cu.* with cross-branches to *R.*, characteristic of *M.*

FIG. 130.—Fore; abnormal; *M.* furcate; *Cu.* crossing branches of *M.* and fusing with *R.*

FIG. 131.—Hind; abnormal; probably owing to a duplication of trachea *Cu.*, the extra trachea becoming associated with *M.*; or, possibly, to a duplication of trachea *M.* and a high development causing a reduction of *Cu.*

FIG. 133.—Fore; abnormal; *M.* duplicated, both stems reduced and fused to *R.*

FIG. 134.—Fore; abnormal; *M.* unusually developed.

PLATE IX.

Cryptotermes, *sp.*

Wings and wing-sac tracheæ.

FIGS. 135A and B.—Wing-stump and base of lamina; fig. 135A, fore wing; fig. 135B, hind wing.

FIG. 136.—Wing-sac of very young nymph, presenting three principal tracheæ (*R.*, *M.*, *Cu.*), which are more or less straight and parallel.

FIG. 137.—Wing-sacs of young nymph, more advanced than that illustrated by fig. 136, presenting five principal tracheæ (*P. sc.*, *C.*, *Sc.*, *R.*, *M.*, *Cu.*).

FIG. 138.—Wing-sacs of young nymph, more advanced than that illustrated by fig. 137, illustrating the development of offsets from *R.* and *Cu.* and the delayed development of the anal.

FIGS. 139A to G.—Diagrams illustrating some of the varied developments of the medial. A, common form; B, medial entwining radial; C, medial departing from radial after becoming applied to it; D, medial with a straight, sector-like branch; E, medial with a sinuate sector; F, medial with a reduced sector; G, sector of medial with two fine branches.

FIG. 140.—Dorsal aspect of cardinal and bases of tracheæ of wing-sac.

FIG. 141.—Wing-sac of a fully-grown nymph with full complement of tracheæ.

FIG. 142.—Apex of wing-sac of a fully-grown nymph, illustrating (1) how the principals extend; (2) how the offsets of the cubital dichotomise and recurve into the field of the wing-sac.

PLATE X.

Cryptotermes, *sp.*

FIG. 143.—Normal fore wing; *M.* with sector-like branch to apex, with cross-branches between *M.* and *R.* and between *M.* and *Cu.*

FIG. 144.—Normal fore wing; *Cu.* strongly developed, with outer branches to *R.*

FIG. 145.—Normal hind wing, with independent rib from apex, probably a disconnected sector-like branch of *M.*; the tip of the medial trachea probably left the radial as in fig. 139c, giving rise to the short inner branch of *R.*

FIG. 146.—Normal hind wing; sector-like branch of *M.* subdivided; two offsets of *Cu.* incurved.

FIG. 147.—Normal fore wing; *Cu.* strongly developed, but on lines quite different from those in fig. 144.

FIG. 148.—Abnormal hind wing; *M.* not attached to *R.*; with an extra rib applied, in part, to *M.*

FIG. 149.—Abnormal hind wing; probably due to a duplication of the cubital trachea.

FIG. 150.—Abnormal hind wing; *M.* duplicated; *M.* not attached to *R.*

FIG. 151.—Abnormal hind wing; extra rib furcate and clearly defined.

FIG. 152.—Abnormal hind wing; *M.* attached at base to *Cu.* instead of to *R.*, with two well-defined, independent ribs between offsets of *Cu.*

FIG. 153.—Cardinal and bases of wing-sac tracheæ, naturally arranged, showing an extra trachea on the base of the radial, which assumes the rôle of an anal after applying itself to the cubital.

FIG. 154.—Illustrating an abnormal development of the tracheæ of the wing-sac; the medial with (1) a well-developed branch crossing the cubital; (2) a branch crossing the radial; (3) a well-developed inner branch.

Rhinotermes putorius.

FIGS. 155 and 156.—*Rhinotermes putorius*; fig. 155, fore wing; fig. 156, hind wing.

FIGS. 157 and 158.—*R. putorius*; wing-stump and base of lamina; fig. 157, fore wing; fig. 158, hind wing.

FIG. 159.—*R. putorius*; wing-sacs of very young nymph, illustrating the development of the tracheæ.

FIGS. 160 to 163.—*R. putorius*; the tracheæ of four wing-sacs of one very young nymph, showing four sufficiently different developments.

FIG. 164.—*R. putorius*; the normal tracheation of the wing-sac of a nearly mature nymph.

FIG. 165.—*R. putorius*; the abnormal tracheation of the wing-sac of a nearly mature nymph, exhibiting an extra principal trachea.

FIG. 166.—*R. putorius*; the cardinal and bases of the tracheæ illustrated in fig. 165.

Psammotermes allocerus.

FIG. 167.—Fore wing with a well-developed media.

FIG. 168.—Hind wing with a well-developed media.

FIGS. 169 to 173.—A series of wings in which the media is absent and the cubitus variously developed.

PLATE XI.

Termes natalensis.

FIG. 174.—Normal wing; *R.* with one sector.

FIG. 175.—Normal wing; *R.* with three sectors.

FIG. 176.—Wing-sac showing tracheation displayed prior to final ecdysis.

FIG. 177.—A part of fig. 176; more enlarged, illustrating the marginal thickening.

FIG. 178.—A part of fig. 176; greatly enlarged, illustrating the subdivision and spreading of the cubital offsets on approaching the marginal thickening.

FIG. 179.—Cardinal trachea of mesothorax, showing the genesis of the trachea of the wing-sac.

FIG. 180.—Cardinal trachea of metathorax, showing a more advanced condition than that of the mesothorax (fig. 179).

FIG. 181.—Wing-sacs of very young nymph, illustrating early form of principals; a post-costal is present in the anterior organ only.

FIGS. 182 to 187.—The cardinal trachea and the basal attachments of the principal tracheæ of the wing-sac as seen in fairly mature nymphs.

FIG. 182.—The post-costal has an independent base between that of the radial and the leg trachea; the anal is well-developed and directed into the thoracic cavity.

FIG. 183.—The post-costal emerges from the base of a bunch of tracheæ which lies well in front of the leg trachea; the base of the radial is fused with that of the cubital; the anal is missing.

FIG. 184.—The post-costal arises from the stock of the radial (as in *Hodo-*, *Calo-*, and *Cryptotermes*); the anal is atrophied.

FIG. 185.—The post-costal is attached similarly to the case illustrated by fig. 184, but is subdivided; the base of the radial is more or less as in the case illustrated by fig. 183; here also the anal is missing.

FIG. 186.—The post-costal is as in figs. 183 and 187; the anal is present but not highly developed.

FIG. 187.—The post-costal as in figs. 183 and 186; the anal has an independent attachment to the cardinal; an atrophied trachea (probably the medial) arises from the base of the cubital.

Microtermes incertus.

FIGS. 188 and 189.—Normal fore wing and hind wing, showing struts between costa and radius.

FIG. 190.—Normal hind wing, with sector to radius.

FIG. 191.—Abnormal fore wing, with *M.* and *Ps. M.* both present.

FIGS. 192 and 193.—Abnormal fore wings with *M.* present, reduced and attached to *R.*

FIG. 194.—Abnormal fore wing; *Ps. M.* attached to *R.*

FIGS. 195, 196, 197.—The cardinal trachea, with buds of wing-sac tracheæ developing.

FIG. 198.—Wing-sacs of a very young nymph, showing early condition of tracheation.

FIG. 199.—Wing-sac of a young nymph in which were the present *Pst. C.*, *Sc.*, and anal.

FIG. 200.—Cardinal trachea and bases of principals, showing an extra trachea (an independent medial) in the presence of a duplicated cubital.

Eutermes (*trinervius* group).

FIG. 201.—Normal fore wing.

FIG. 202.—Abnormal fore wing (the companion of fig. 201) with a duplicated media.

FIG. 203.—Cardinal and bases of principal tracheæ of wing-sac, as seen in young nymphs.

FIG. 204.—Cardinal and bases of principal tracheæ of wing-sac, as seen in older nymphs; *M.* and *Cu.* closely applied.

Microtermes *sp.*

FIG. 205.—The cardinal and bases of principal tracheæ of wing-sac; the root of *R.* abnormally close to that of *M.*

Cubitermes bilobatus.

FIG. 206A.—The cardinal with bases of principal tracheæ of wing-sac; the radial bearing (abnormally) a vestigial post-costal.

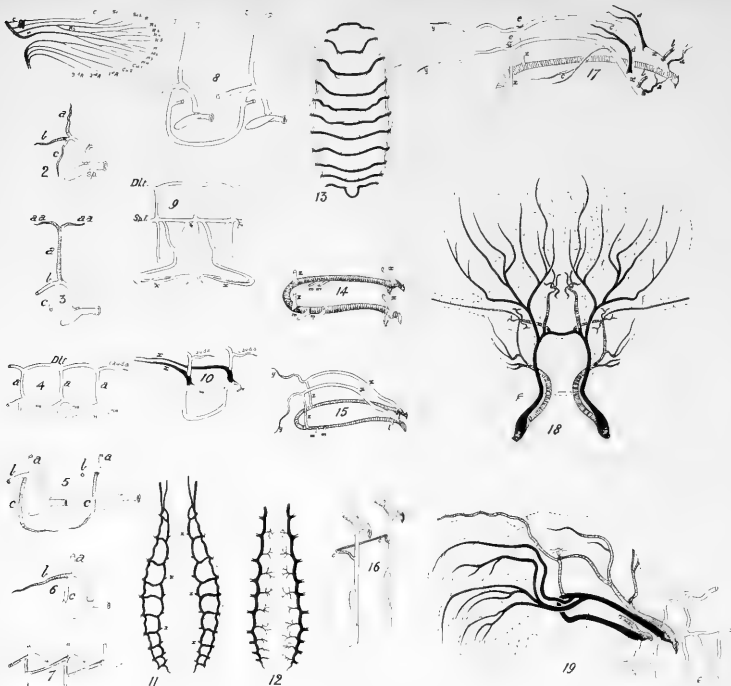
FIG. 206B.—An enlarged view of the vestigial post-costal of fig. 206A.

Hamitermes hastatus.

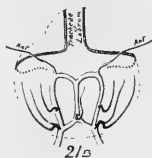
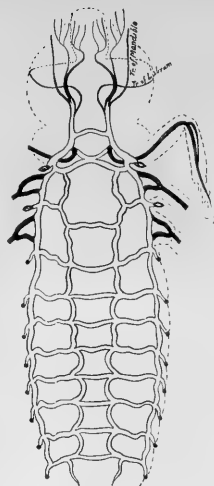
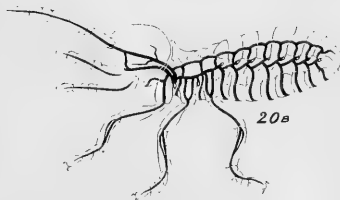
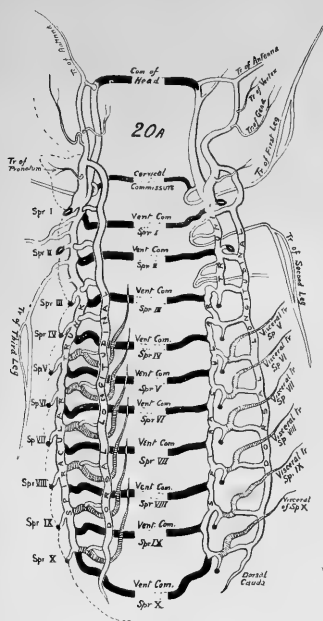
FIG. 207.—The cardinal and bases of the principal tracheæ of wing-sac; also the bases of the leg trachea and of the bunches of thoracic tracheæ.

Promirotermes sp.

FIG. 208.—Wing-sac with three normal tracheæ (in solid block) and an extra trachea (? medial), also an unusually large branch to the cubital.

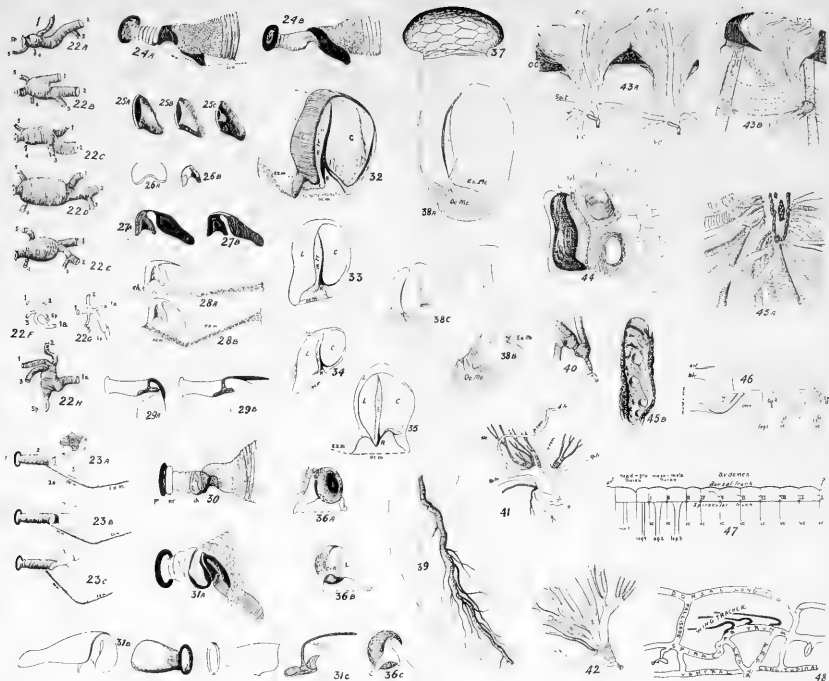


TERMITE TRACHEAL SYSTEM



Mandibles of *Eutermes*

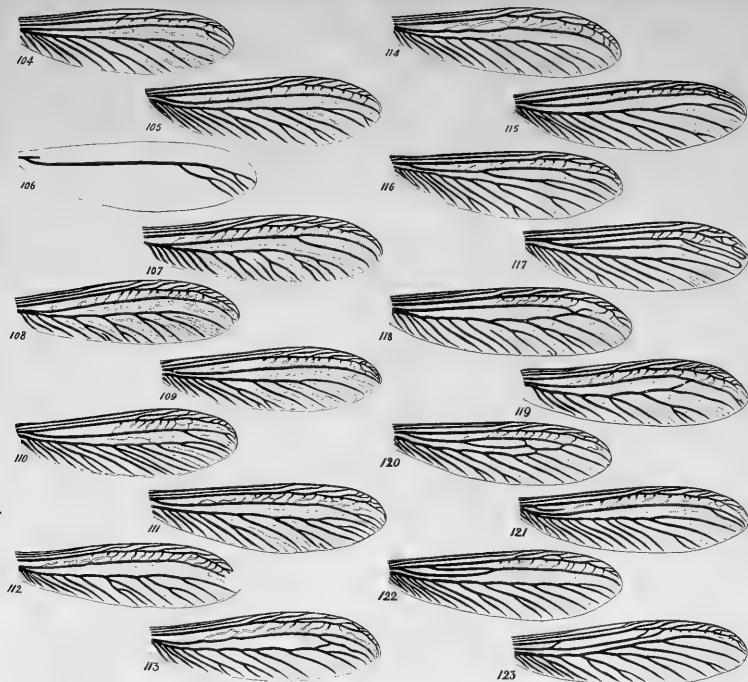
TERMITE TRACHEAL SYSTEM



TERMITE SPIRACLES AND WING TRACHEÆ

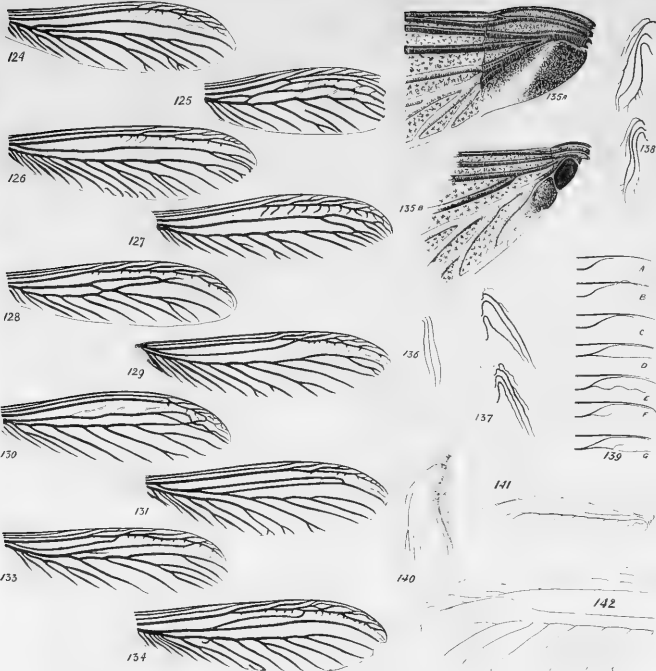




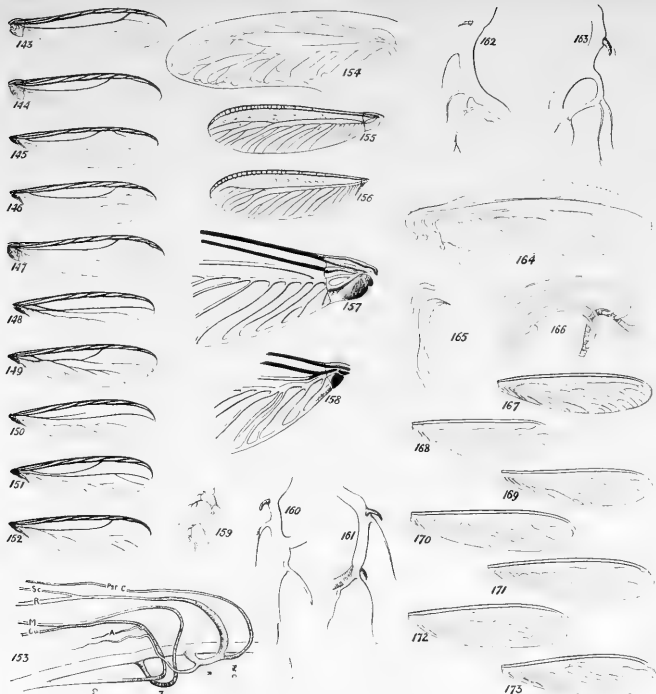


WING VENATION OF *CALOTERMES DURBANENSIS*



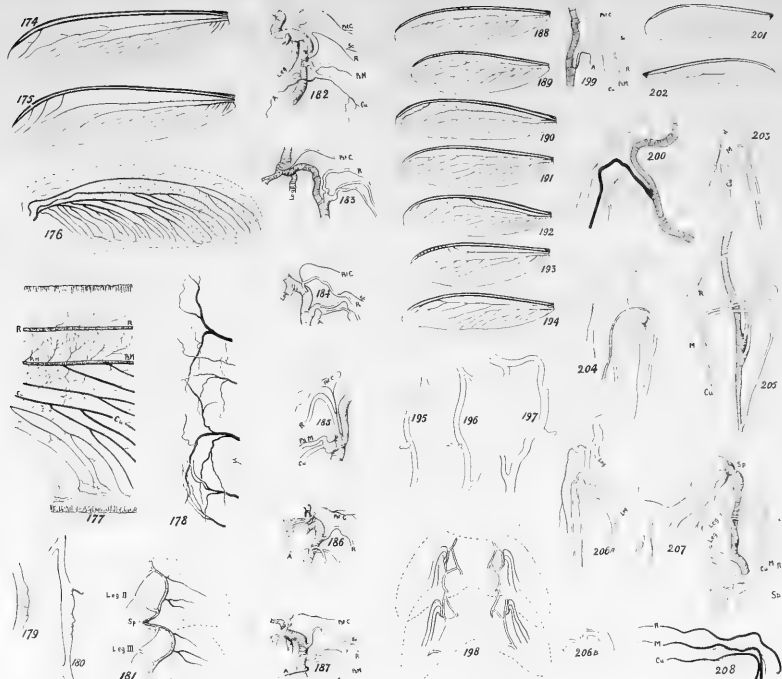


CALOTERMES DURBANENSIS (FIGS. 124-134), *CRYPTOTERMES* SP. (FIGS. 135-142)



CRYPTOTERMES SP. (FIGS. 135-154), RHINOTERMES PUTORIUS (FIGS. 155-166),
PSAMMOTERMES ALLOCERUS (FIGS. 167-173)





TERMES NATALENSIS. (FIGS. 174-187), MICROTERMES INCERTUS (FIGS. 188-200), EUTERMES (FIGS. 201-204), MICROTERMES SP. (FIG. 205),
CUBITERMES BILOBATUS (FIG. 206), HAMITERMES HASTATUS (FIG. 207), PROMIOTERMES SP. (FIG. 208)

Observations on Cellular Degeneration and the Formation of Pigment in certain Hydroids.

By

Ernest Warren, D.Sc.(Lond.).

With Plate XII and Text-figs. 1-11.

IN the examination of hydroids collected on the eastern coast of South Africa it has been noticed that, in the case of certain species, black, or very dark brown, colonies occasionally occur in addition to those of the usual pale horn or yellowish-white tint. This black condition of some of the colonies was first noticed in 1905, when local specimens of *Sertularia loculosa* Busk from the Natal coast had been collected, and in a description¹ of the specimens the matter was referred to in the following terms: "In the black variety the endoderm is provided with dark brown, opaque, pear-shaped masses. These are, doubtless, cells, but I have not with certainty detected the nucleus. The colouring matter may be very opaque and compact, but sometimes it is seen in the form of granules."

Subsequently a similar condition has been found in a number of other species, and a careful histological examination has led to the conclusion that the development of the pigment is the result of a disturbance in the physiological functions. The phenomenon is not uncommon among South African hydroids, and there is no reason to suppose that it is in any way peculiar to them.

¹ 'Annals of the Natal Mus.,' vol. i, pt. 3, p. 308, 1908.

The manner of the production of the pigment or coloured substance and the kind of cells affected vary in the different species, but in all cases the whole or a portion of the cell producing it dies, and more frequently the colony appears to be in a somewhat weak and sickly condition, although not necessarily moribund.

THE CAUSES OF PIGMENTATION.

The material at my disposal, and the lack of opportunity for extended observations on the sea-shore, preclude any final statement as to the cause or causes of the phenomenon. There is, however, some evidence for suggesting that excessive insolation is one of the agents in inducing the pigment-degeneration in the cells. Another factor which certainly favours it, and perhaps at times is sufficient in itself, is the senescence of the colony. A third possible cause is the continued stimulation of the colony by the agitation of the water between the tide-marks, and another conceivable factor is the stimulus arising from the partial dessication which may periodically occur when colonies are left exposed by the receding tide. As far as my observations go, the coloured colonies appeared to be especially those which were of considerable age and which happened to be exposed to the direct sunlight and to the buffeting of the waves. The material examined was mostly obtained from the rocks between the tide-marks, and the few specimens collected by trawling in deep water belonged to species in which pigment-degeneration has not been observed. It would be of interest to compare specimens of the same species collected on the shore and from deeper water in order to estimate the effect of insolation.

Senescence of the colony would, however, appear to be an undoubted factor. Old and large colonies tend to exhibit the condition in a far more striking manner than young, small colonies. The young, growing parts of an old, mature colony may show considerable pigmentation, and it would therefore appear that the vital activity of the colony as a

whole may become so reduced that even in those parts where a certain amount of new growth is occurring the physiological functions are not completely normal in character. Notwithstanding this, however, the older portions of the colony show much greater pigmentation than the younger portions.

I can find no clear evidence that the pigmented condition is associated with the presence of any parasitic organism. Bacteria and parasitic protozoa were carefully searched for in all the preparations, but no certain trace of their occurrence could be detected. The rodlets of pigment seen in unstained preparations of *Sertularia operculata* certainly mimic stained bacteria in an extraordinary manner; but their mode of origin negatives the view that they are of bacterial nature.

To distinguish and separate the agencies involved in this pigment-degeneration, experiments with living hydroids would be of great interest; but the facilities of a marine laboratory would be essential before the investigation could be undertaken.

The study of cellular degeneration in a simple organism with a relatively simple histological structure is of some interest, as it is likely to lead to a better understanding of the phenomenon as it occurs in higher animals and in man himself.

We know that in the case of white man exposure to the sun usually induces freckles and a general darkening of the skin. This condition is due to the presence of melanin granules in, and between, the epithelial cells. At the present time it is more generally held that the melanin is actually produced by the epithelial cells, and is not, as was formerly thought, brought to them by wandering mesoderm cells which had elaborated it from the hæmoglobin of the blood. The melanin granules are often found between the epithelial cells, and if the granules had become scattered by the disintegration of some of the pigment-producing cells, we should arrive at a condition which is closely paralleled by that which is sometimes seen in hydroids. It is not to be supposed, however,

that the melanin of vertebrates is of the same chemical nature as the black and brown pigments of hydroids and other invertebrates.

THE NATURE OF THE PIGMENT.

Our knowledge of the origin and chemical nature of the pigments occurring in animals is still deficient. The black pigment, commonly known as melanin, found in vertebrates, appears to have a chemical constitution related to that of hæmoglobin. It is certain that the various colouring matters found in invertebrates are not all similar to one another in chemical character, and doubtless they differ considerably from the melanin of vertebrates.

I have tried a few microchemical and other tests on the dark brown pigmented cells of *Lytocarpus filamentosus*, and the following is a summary of the results. In considering these reactions, however, it must be remembered that the specimens had been fixed several years previously with corrosive sublimate and acetic acid.

- (1) The pigment granules had no effect on polarised light.
- (2) Weak acids and weak alkalis of about 20 per cent. strength had no definite effect on the granules.
- (3) Alcohol, benzole, oil of cloves, and ether had no action.
- (4) Chlorine dissolved in alcohol decolourised the granules, so also did 50 per cent. hydrochloric acid which had become yellow by the formation of free chlorine.
- (5) Peroxide of hydrogen had a somewhat weak decolourising action.
- (6) Osmic acid did not appear to intensify appreciably the colour of the granules.
- (7) Millon's reagent tinged red any granules which happened to be less dark coloured than usual.
- (8) Concentrated nitric acid decolourised the granules instantly, and they became yellow; the yellow colour was intensified by the addition of ammonia.
- (9) A saturated solution of nickel sulphate in ammonia

gave a yellowish coloration to granules which were not considerably blackened.

(10) The Biuret test, consisting of treatment with concentrated sulphate of copper followed by concentrated potash, gave no very characteristic result. The black coloration disappeared at once, and the granules became yellow or reddish-brown; but concentrated potash by itself gave a similar reaction, although not so marked.

(11) A weak solution of iodine in iodide of potassium gave a faint yellowish reaction.

(12) As a test for iron the sections were treated with alcohol containing 4 per cent. sulphuric acid and 3 per cent. nitric acid. After washing with pure alcohol and water, the preparations were treated with a solution consisting of 1·5 per cent. ferrocyanide of potassium and 0·5 per cent. hydrochloric acid. The coloured granules exhibited no blue coloration, and accordingly the test gave a negative result.

(13) The granules had no marked affinity for eosin when applied in the form of a weak aqueous solution, but they were faintly tinged by the stain.

Taking these reactions altogether, the coloured granules would appear to be of a proteid nature. As already intimated, the formation of pigment in hydroids is probably not to be regarded as arising through the presence of bacteria or other organisms, but it would seem to be due to a disturbance in the metabolism of the cell, which results in the production of a coloured substance in a manner resembling amyloid and colloid degeneration and the calcification of cells.

In speaking of metamorphic processes in cells, Verworn¹ states: “. . . the metabolism of the cell does not merely come gradually to a standstill, but is previously turned into a perverse course in such a way that substances which in the normal cell are either not manufactured at all, or appear only as intermediate stages, are produced in quantity as a result of the disturbed metabolism, and accumulate within

¹ Verworn, Max, ‘General Physiology,’ English transl., London, 1899, pp. 330–331, 336.

the cell until the latter perishes." Verworn mentions fatty degeneration, mucous degeneration, amyloid degeneration, calcification, pigment-atrophy, hyaline degeneration, and colloid metamorphosis.

DISTRIBUTION OF THE PIGMENT.

In dealing with the different species it will be seen that all the tissues of the hydroid are not always involved in this pigment-degeneration. Sometimes only certain tissues, or particular kinds of cells, or portions of cells, are transformed. Thus the stimulus does not necessarily cause pigment-degeneration in all the cells of the body or even in all parts of the same cell, and this implies that it produces an effect only when the protoplasm is in a certain physiological condition. There is a curious tendency for the transformed cell, portion of cell, or collection of cells to assume a characteristic shape in the different species; e. g. in *Sertularia loculosa* the brown pigment masses are usually more or less pear-shaped, and in *Sertularia operculata* they may form narrow streaks or a reticulum stretching through the living protoplasm of several ectodermal cells.

Before discussing the matter further it will be well to give some account of this pigment-degeneration as it occurs in several species. It has been observed in various degrees of intensity in the following species:

- (1) *Lytocarpus filamentosus* (*Lam.*).
- (2) *Thuaria tubuliformis* (*M. Turn.*).
- (3) *Sertularia operculata* *Lin.*
- (4) *Sertularella mediterranea* *Hartl.*
- (5) *Sertularia linealis* *Warren.*
- (6) *Sertularia loculosa* *Bale.*
- (7) *Paragattya intermedia* *Warren.*
- (8) *Sertularia bidens* *Bale.*
- (9) *Kirchenpaueria mirabilis* (*Allman*).

(1) *Lytocarpus filamentosus* (*Lam.*).

Pl. XII, figs. 1-3; text-figs. 1-3.

In this species both dark brown or black specimens and pale horn-coloured colonies occur. The pigmented specimens were found in bare exposed pools at Alexandra Junction, Natal, and at Sisters' Rock, Port St. John, Pondoland. The colonies were 4-5 in. in length and were clearly of considerable age. The non-pigmented specimens were found at Park Rynie, Natal, in sheltered pools considerably overgrown with weed; they were small, young colonies, not more than about $1\frac{1}{2}$ in. in height.

The pigmented colonies were not in a vigorous condition; a good many of the polyps appeared to be moribund, and some portions of the colonies were completely dead. A microscopic examination showed that the blackness arose through the fact that large numbers of both the ectoderm and endoderm cells were densely crowded with relatively large, dark brown granules (Pl. XII, figs. 1-3).

In text-fig. 1, A, a fairly vigorous polyp and a piece of the cœnosarc are illustrated in longitudinal section. Pigmented areas of considerable size are seen in the endoderm, in the general ectoderm, and in the thin, outer sheets of ectoderm. Mostly these areas correspond to separate cells which assume an oval shape, but sometimes there is formed a reticulum of pigmented strands consisting of several cells or portions of cells. In fig. B are seen two endoderm cells and an ectoderm cell in process of transformation. Figs. C-G illustrate the stages of transformation of an ectoderm cell in the outer ectoderm sheets¹ seen in fig. A.

Usually the pigment granules appear in little clusters in

¹ It may be mentioned here incidentally that these thin, outer ectoderm sheets would appear to functionate as structures by means of which the cœnosarc and polyps may cling to the inner surface of the perisarc-tube and hydrothecæ. In the case of operculate species of *Sertularia* these sheets around the polyp are supposed to serve as opercular muscles.

the cytoplasm and a progressive disappearance of the living protoplasm gradually occurs (fig. c), until the entire cytoplasm may become involved. Later, the chromatin disappears and the nucleus becomes clear except for the nucleolus which persists (figs. e and f). In fig. g the nuclear membrane has become dissolved and the loose nucleolus can be seen in the dying cell; definite, irregularly-shaped cavities may be formed in the cell. A similar transformation can be followed in the endoderm cells (figs. h-k).

The granules are refringent and appear to be surrounded by a fairly thick layer of a substance having the appearance of mucus which does not readily stain (text-fig. 3, b). These layers become continuous where many granules are present. Such a collection of granules mimics in a diminutive form a zooglea mass of cocci (text-fig. 3, a). The jelly or mucus-like substance is somewhat refringent, but less so than the granules.

Some sections were stained by the Kühne-Grammethod for bacteria. Such granules as had not become very dark brown in colour were tinged light purple, while the clear matrix surrounding the granules assumed a very faint but definite yellow tinge.

It may be said by some that these so-called refringent granules are simply parasitic cocci; and possibly the late Dr. C. Bastian would have contended that we are here witnessing the transformation of the protoplasm of the cells of the hydroid into some primitive type of life.

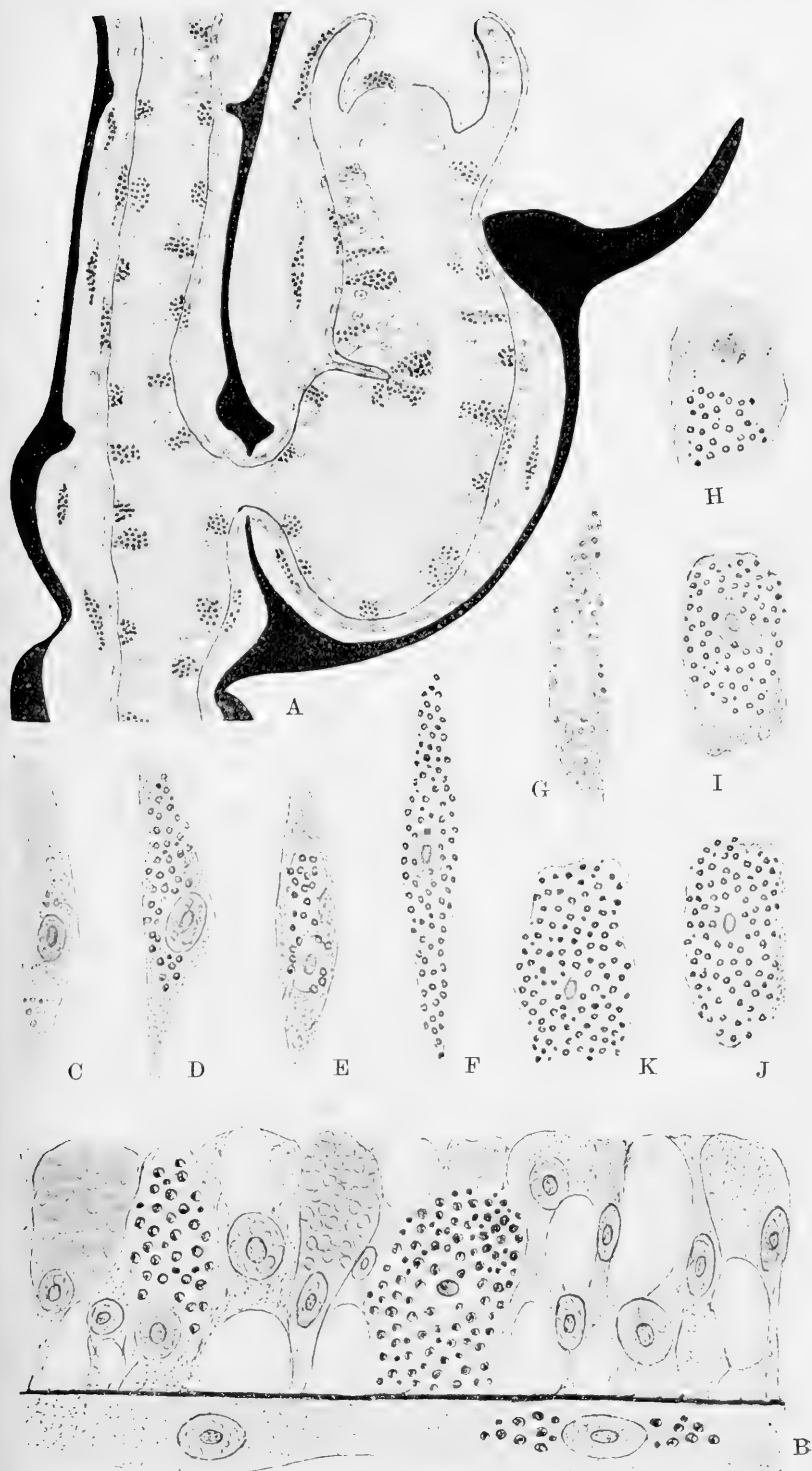
Although Bastian's ideas are still generally regarded as heresy, I am not prepared to combat the main principle of his views; but more evidence is undoubtedly required.

That the granules are ordinary cocci appears very unlikely for the following reasons:

- (1) They have no constant size; the granules vary from the limit of visibility with a Zeiss apochromatic (1.5 mm.) to a diameter of about 0.7μ .

Fig. 1.—*Lytocarpus filamentosus*. Fig. A, $\times 270$. Fig. B, $\times 1300$. Figs. c-k, $\times 1100$.

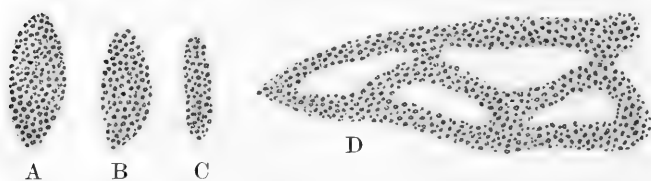
TEXT-FIG. 1.



(2) No budding or division of the bodies could be detected with any certainty; no chains nor diplococci were seen.

(3) There is a marked tendency for individual cells surrounded by ordinary healthy tissue to be pigmented,

TEXT-FIG. 2.

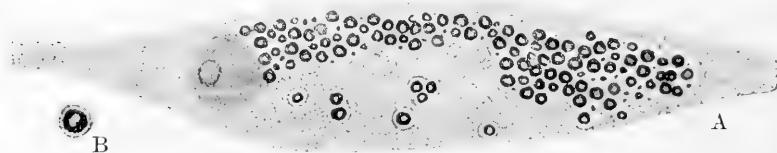


Lytocarpus filamentosus. $\times 750$.

while in the case of bacterial infection continuous areas would probably be involved.

From these considerations it may be presumably assumed that the granules in question and the surrounding clear

TEXT-FIG. 3.



Lytocarpus filamentosus. Fig. 1, ectoderm cell, $\times 2500$.

Fig. 2, single granule, $\times 5000$.

mucilage-like substance result from the transformation of the living protoplasm.

Such transformation gradually increases until almost the whole of the tissues may become affected. The masses of granules, whether resulting from one cell or several contiguous cells, generally assume an oval shape whatever the original shape of the cell (text-fig. 2, A, B, C). At times the masses run into one another and an irregular reticulum results (fig. D). By this time the tissues affected have become moribund and ultimately perish.

(2) *Thuiaria tubuliformis* (*M.-Turn.*).

Pl. XII, figs. 4, 5; text-figs. 4, 5.

This hydroid is one of the commonest on the Natal coast. It is abundant in the form of small, short colonies attached to the bare surface of rock. In certain situations the colonies are left exposed to the air for some time during low-water. As a matter of fact, this species is subjected more markedly than any other to: (1) intense insolation, (2) periodical buffeting by the waves, (3) periodic partial dessication. I have not been able to separate satisfactorily the effects of these various agents; but there is no doubt that unfavourably placed colonies are particularly liable to pigment-degeneration.

In Pl. XII is shown the general aspect of a portion of a colony in which the degeneration is beginning (fig. 4) and in which it is in an advanced condition (fig. 5).

The nature of the pigment-degeneration differs appreciably from that described in *Lytocarpus filamentosus*. The degeneration is less confined to individual cells than in that species. A group of cells or portions of cells becomes involved and there are formed elongated masses or narrow streaks of vacuolated, blackened material extending through the living tissue.

The degeneration first begins by the formation of pigment granules enclosed by a mucilage-like layer. When a number of granules are formed close together there results a soft unstainable (e. g. with carmine and hæmatoxylin) patch in the cytoplasm crowded with dark brown or black pigment granules. These granules are much smaller than in *Lytocarpus*, being about half the size. They are also much blacker, and consequently far more opaque and less refringent (text-fig. 4, D). The protoplasm of the cell becomes conspicuously vacuolated and honeycombed and the granules accumulate around the walls of the cavities, forming a dense black edging. Text-fig. 4, J-M, represents the changes in a

group of endoderm cells. The nuclei of the cells lose their chromatin, tend to become homogeneous and ultimately disappear.

There may be a marked hypertrophy of the cells, as is shown in figs. f, g, where one or more ectoderm cells have formed an eruption three or four times the height of the ectoderm layer.

In cross-section of the cœnosarc there are seen in the endoderm large, oval, honeycombed areas with blackened walls, taking the place of a number of cells, and with their long axis pointing towards the centre (fig. b). In fig. e an example is illustrated where vacuolation is late in appearing. In figs. h and i pigment granules are being formed in immediate contact with an endoderm nucleus, and in fig. i the nucleus has become homogeneous in character. In figs. n-p the course of change in an endoderm gland-cell is shown. The normal rounded masses of secretion are shown in fig. n; in fig. o the beginning of pigment formation and vacuolation is seen in the middle of the cell, and in fig. p the condition is much more advanced. The ordinary cytoplasm of the cell is not completely involved even in fig. p, but the nucleus has become homogeneous and apparently moribund.

In surface view of the hydroid the areas involved in this degeneration in the endoderm are rounded, oval, or often spindle-shaped in outline (text-fig. 5, A, B) and of moderately uniform size (long axis about 15μ). Sometimes elongated, rather thick bands are formed (text-fig. 4, A and 5, c). In the ectoderm the areas are usually narrow, elongated, or fusiform (text-fig. 5, D-H).

The long axes of the elongated blackened areas in the endoderm are in the long axis of the cœnosarc. The narrow streaks in the ectoderm are also frequently in the long axis, but sometimes they may lie more or less transversely (text-

Fig. 4.—*Thuiaria tubuliformis* (M.-Turn.). Fig. A, $\times 425$.
Fig. B, $\times 1200$. Fig. c, $\times 900$. Fig. D, $\times 10,000$. Fig. E, $\times 1200$.
Fig. F, $\times 1400$. Fig. G, $\times 700$. Fig. H, $\times 2000$. Fig. I, $\times 1200$.
Figs. J-M, $\times 1500$. Figs. N-P, $\times 1600$.

TEXT-FIG. 4.

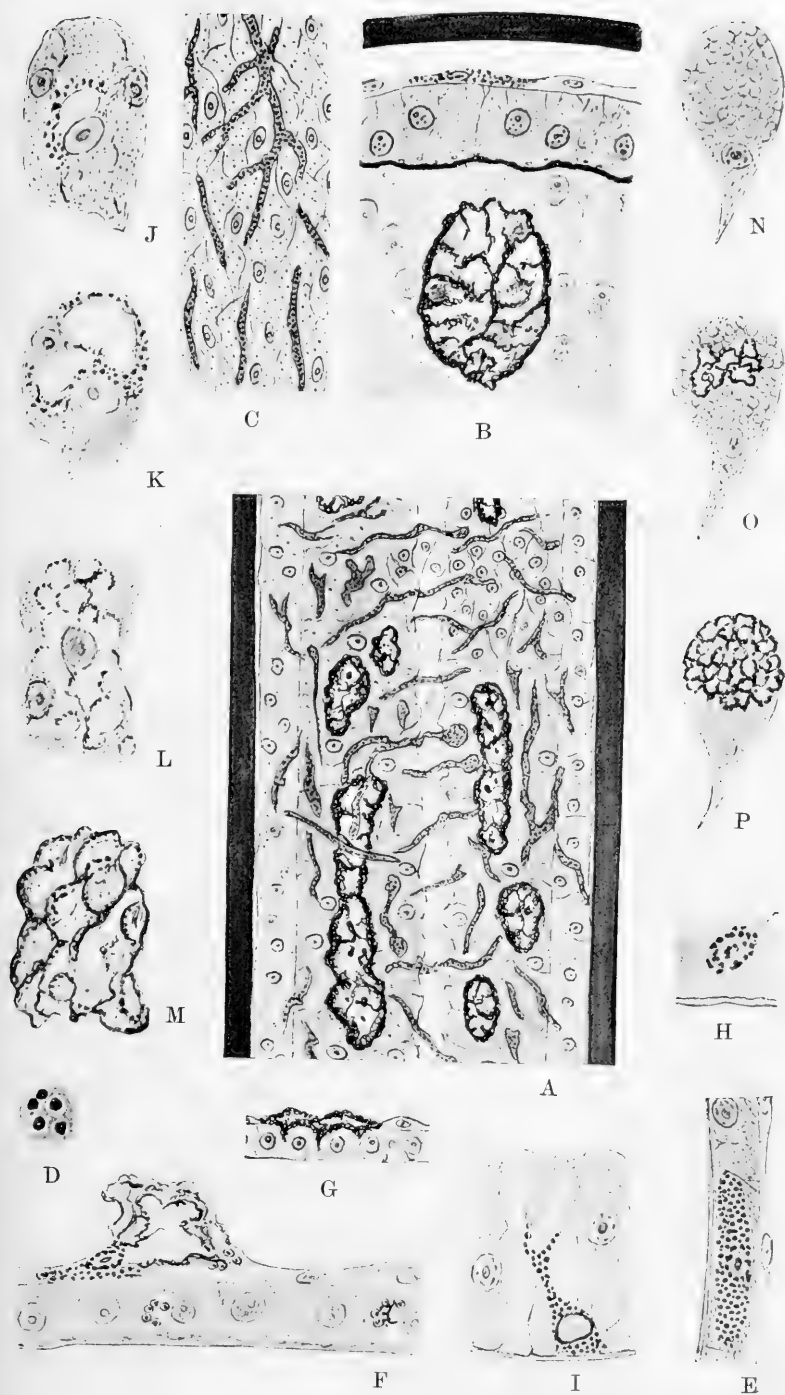
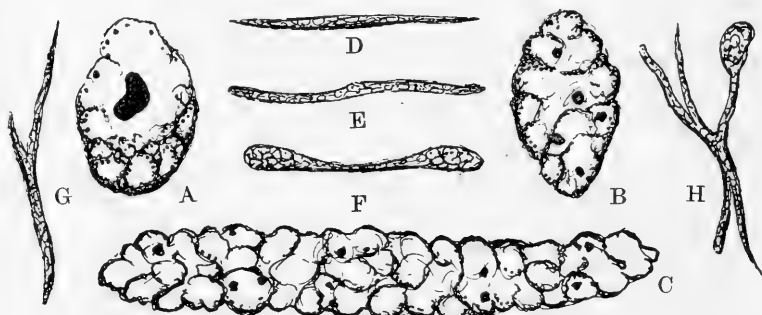


fig. 4, A). It is pretty clear that these streaks do not necessarily correspond to the outlines of cells, but they involve several cells or portions of the same.

Sometimes, and especially in the endoderm, in place of the walls of the vacuolated cytoplasm being conspicuously blackened, the pigment becomes concentrated in somewhat large, irregularly shaped lumps which subsequently lie loose

TEXT-FIG. 5.



Thuiaria tubuliformis (M.-Turn.). $\times 1200$.

in the vacuoles, and are very opaque (text-fig. 5, A-C). As a result of this degeneration, the areas form leopard-like spots (Pl. XII, fig. 4).

(3) *Sertularia operculata* Lin.

Pl. XII, figs. 6-8; text-fig. 6.

Most of the colonies collected between the tide-marks on the Natal coast exhibited pigment-degeneration to a greater or lesser degree, but one or two small young colonies were practically free from it. In a specimen received from Plymouth, England, a certain amount of degeneration was observable.

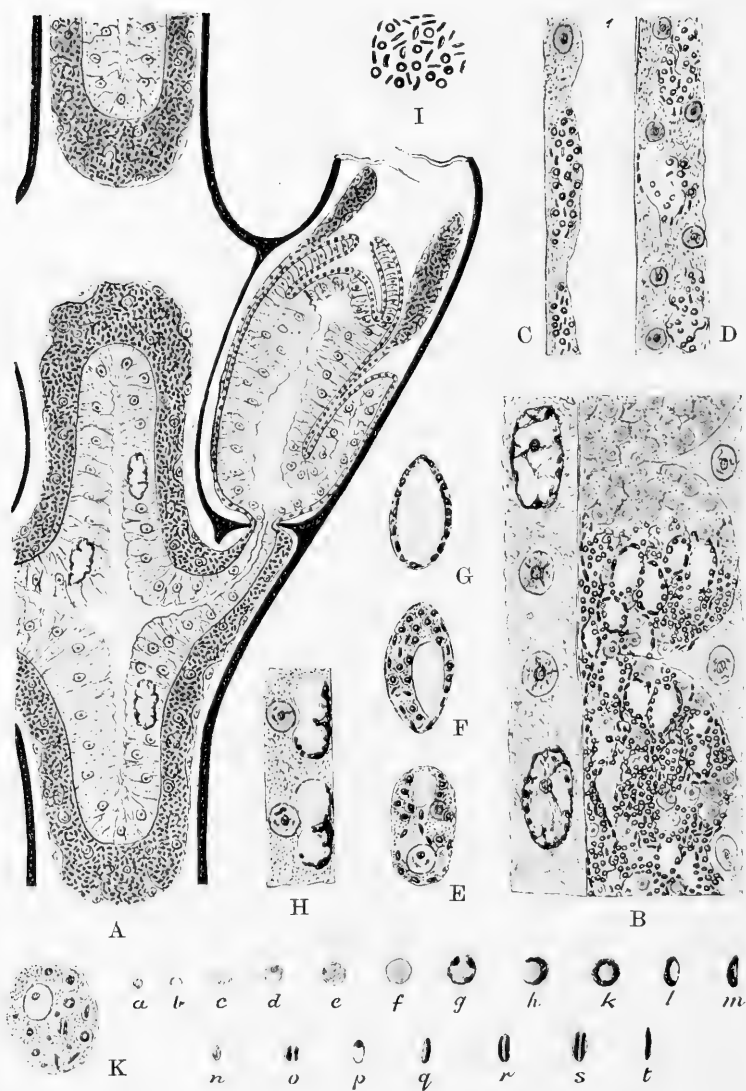
In older colonies the degeneration may become excessive, especially in the ectoderm of the cœnosarc (Pl. XII, figs 6-8), and it appears to lead to the formation of actual divisions

of the cœnosarc-tube. These breaks seemed to occur more frequently towards the extremities of the branches than in the main stem. The constrictions are formed in the cœnosarc above and below a pair of hydrothecæ (Pl. XII, fig. 8; text-fig. 6, A). A rough broken surface exposing the endoderm is not present, but a complete covering layer of ectoderm is formed, and the hydranths can be seen to be in a living condition. Some hypertrophy of the ectoderm and of the so-called muscular sheet of the hydranth can be observed (text-fig. 6, A). Ultimately the cœnosarc and hydranths succumb and the tissues are reduced to isolated masses and strands of a black substance.

A considerable portion of the ectoderm of the cœnosarc is greatly thickened owing to the multitude of interstitial cells. The myo-epithelial elements form an outer epithelium of large cells which rapidly taper inwards (fig. B). The interstitial cells are particularly liable to pigment-degeneration (fig. B), although it is also found in the thin ectoderm layer of the hydranth (figs. C and D).

The pigment granules formed in the ectoderm are of considerable size ($1.0\ \mu$), and they are dark brown or black. They are of a peculiar character, consisting of little, flat, round plates and of bacterium-like rods (figs. I and K). Some zoologists may insist upon the view that these structures are really parasitic organisms; but they arise in the cells in a manner quite similar to that in which pigment granules, which do not mimic organisms, arise in other hydroids, and accordingly I doubt whether they are independent organisms. It is true that sometimes the rodlets may be seen in lines (fig. D, middle of figure) as if the individuals had arisen by transverse fission; but the structures are black, the microchemical tests for fungus-cellulose were inconclusive, and no iron was detected. The size of the largest of the coccus-like granules ($1.0\ \mu$) is about that of ordinary cocci, but the bacterium-like bodies ($1.3\ \mu$) are smaller than most bacteria. There was no conclusive evidence of the division of the granules into chains or "diplococci." Also, the granules vary greatly in size.

TEXT-FIG. 6.



Sertularia operculata Linn. Fig. A, $\times 220$. Fig. B, $\times 900$.
 Figs. C-H, $\times 1100$. Figs. I, K, $\times 1700$. a-t, $\times 5500$.

A study of the structure and mode of development of the pigment granules would seem to show that they gradually arise in the protoplasm of the hydroid cell from the limit of visibility until a colourless corpuscle of considerable size is formed (text-fig. 6, κ , $f.$). Subsequently the corpuscle darkens by a further decomposition of the proteid, and the actual colouring matter arises. This black or dark brown substance may be especially concentrated in small lumps ($g.$) in the corpuscle, or it may form a crescent or ring around the periphery of the corpuscle ($h.$, $k.$). Instead of forming a disc the body may be rod-like and the black substance may be concentrated in the form of two black parallel streaks ($o.$, $r.$, $s.$). Many may be tempted to believe that this is really some stage of fission of a simple schizophyte; but, as stated above, it is very doubtful whether these discs or rodlets can be rightly regarded as parasitic organisms foreign to the tissues of the hydroid.

In the ectoderm a single cell, or a cluster of several, produces the pigment granules in a similar manner to that described in *Lytocarpus filamentosus* and *Thuiaria tubuliformis*. The granules appear in the protoplasm surrounded by a halo of unstainable substance which is apparently mucilaginous (fig. κ). The mucilage coat, however, is more evanescent than in the other species, and in granules that have become isolated from the protoplasm it does not appear to remain attached to the granule as a definite layer, and consequently zooglea-like masses are not obvious. Cavities form early in the cell or cluster of cells, and these tend to run into one central cavity which is densely surrounded by the pigment granules. The nucleus or nuclei disappear. There is usually formed an oval sac measuring some $9.2\ \mu$ in the long axis (figs. b , e , f and g).

In the endoderm the formation of pigment granules is much less conspicuous; a few granules may be formed in a cell or in an oval area formed by several cells or portions of cells. Very soon large vacuoles occur, and the pigment substance is deposited as an irregular layer or in small lumps

on the walls of the expanding cavities (text-fig. 6, A, B). In fig. H the pigment-degeneration is seen proceeding in the inner portion of two contiguous endoderm cells.

(4) *Sertularella mediterranea* Hartl.

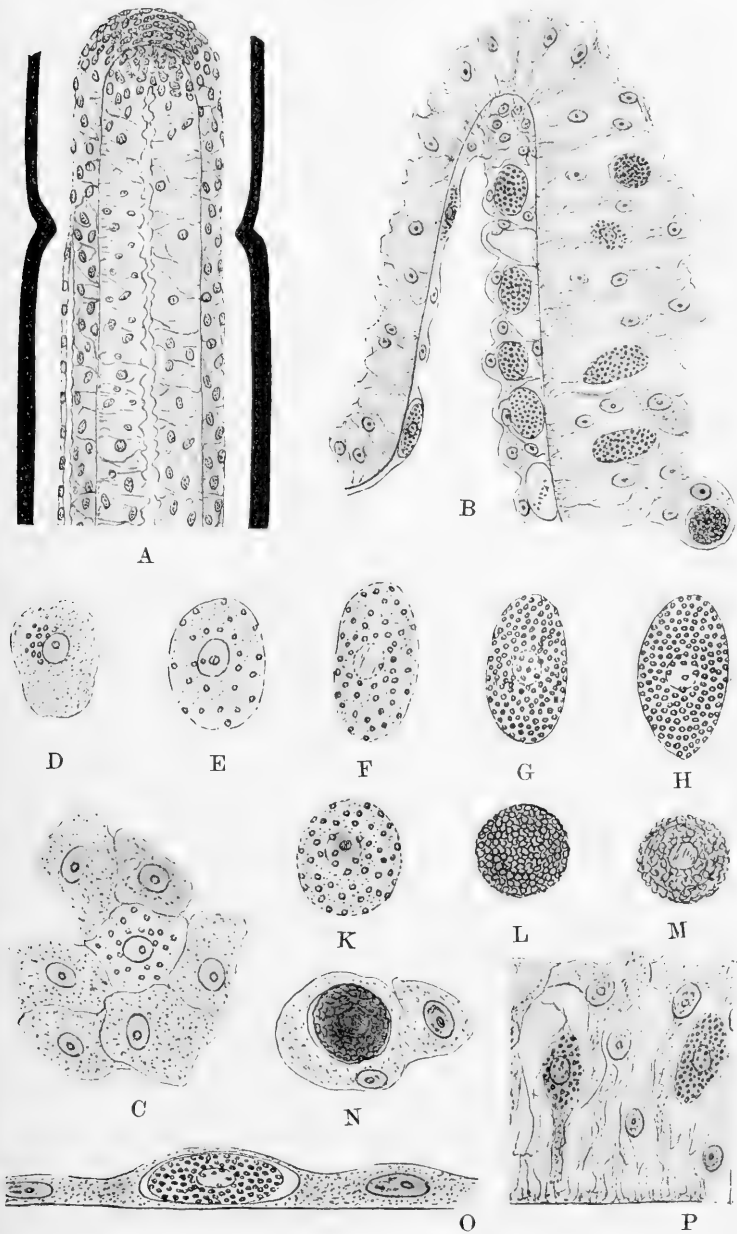
Text-fig. 7.

This common species on the Natal coast exhibits a type of pigment-degeneration which differs considerably from the kinds of degeneration already described. Older, exposed colonies appear yellowish-green to the naked eye. Microscopical examination shows that this condition results from the presence of more or less numerous oval-shaped areas which contain small yellowish granules (text-fig. 7, A, B). In *S. mediterranea* these areas generally represent a single transformed cell, or sometimes, perhaps, a portion of a cell only, while in *Lytocarpus filamentosus*, *Thuiaria tubuliformis*, and *Sertularia operculata* the modified areas may mostly consist of several cells. The series of changes which these cells undergo are illustrated in text-fig. 7, C-N. As the granules arise the general cytoplasm becomes less turbid and stains less readily with hæmatoxylin (figs. C, D). The nucleus undergoes change and the chromatin disappears, so that the nucleoplasm becomes clear except for the nucleolus which seems to remain unaltered for a time. Subsequently even the nucleolus cannot be found and the nucleus is seen to be quite homogeneous (F). The granules increase in number and the cells become oval whatever the original shape of the cell (figs. E-H). The protoplasm is gradually converted into yellow granules of average diameter about $0.4\ \mu$, and into a transparent matrix.

On staining by the Kühne-Gram method the granules became reddish-yellow and the matrix a fairly dark yellowish-brown. Sometimes the areas are almost perfectly spherical (fig. K), and the granules may be exceedingly concentrated,

Fig. 7.—*Sertularella mediterranea* Hartl. Fig. A, $\times 220$. Fig. B, $\times 1100$. Figs. C-O, $\times 3000$. Fig. P, $\times 1700$.

TEXT-FIG. 7.



and later they appear to fuse together partially or completely to form a compact ball (fig. M). It is not always clear that the spherical bodies invariably correspond to a single cell, sometimes they appear to consist of a modified portion of the cytoplasm of a single cell, which rounds itself off and is converted into a spherical mass embedded in the general protoplasm of the living cell (fig. N).

The bodies measure about $8\ \mu$ in the long axis and are mostly of a somewhat elongated oval in shape. They do not differ greatly in shape or size, whether they are in the ectoderm (fig. O) or endoderm (fig. P). A superficial examination might readily enough lead to the supposition that the structures are parasitic protozoa or symbiotic algæ with yellow chlorophyll corpuscles; but the greenish colouring matter appears to be quite insoluble in alcohol, and every stage can be traced in the transformation of a tissue cell into these yellow bodies. For these reasons the yellow bodies are regarded as similar in general character to the black pigment areas of the species previously described.

(5) *Sertularia linealis* Warren.

Text-fig. 8.

In the few available specimens of this species there occurred but little pigment-degeneration, but in one specimen a certain amount was found in the ectoderm (text-fig. 8). The degeneration was of the type of a vacuolated protoplasm with the walls lined by a deposit of black pigment. In this specimen practically no degeneration was found in the endoderm. The degeneration areas would seem to comprise a group of interstitial cells.

(6) *Sertularia loculosa* Bale.

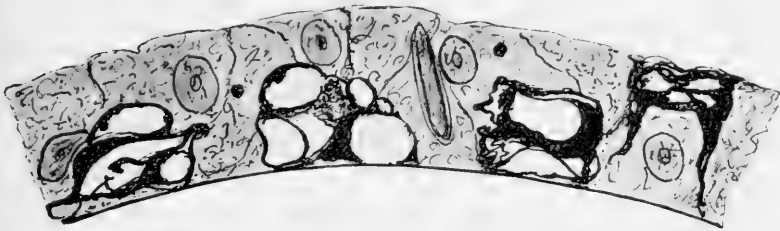
Text-fig. 9.

The type of pigment-degeneration is very distinctive in this species. In the black specimens pear-shaped, dark brown bodies are found both in the ectoderm and endoderm

(text-fig. 9, A-G). In this condition no nucleus can be detected.

These curious bodies are transformed cells or portions of cells. In text-fig. 9, A and B, early stages in the formation of the bodies can be seen. The whole cell tends to become pear-shaped, or a pear-shaped area becomes differentiated around the nucleus. In this area relatively large ($0.8\ \mu$), rounded, pale brown globules are gradually formed (text-fig. 9, c). The globules increase in number (fig. d) and the nucleus becomes clear and does not stain readily. Sometimes,

TEXT-FIG. 8.



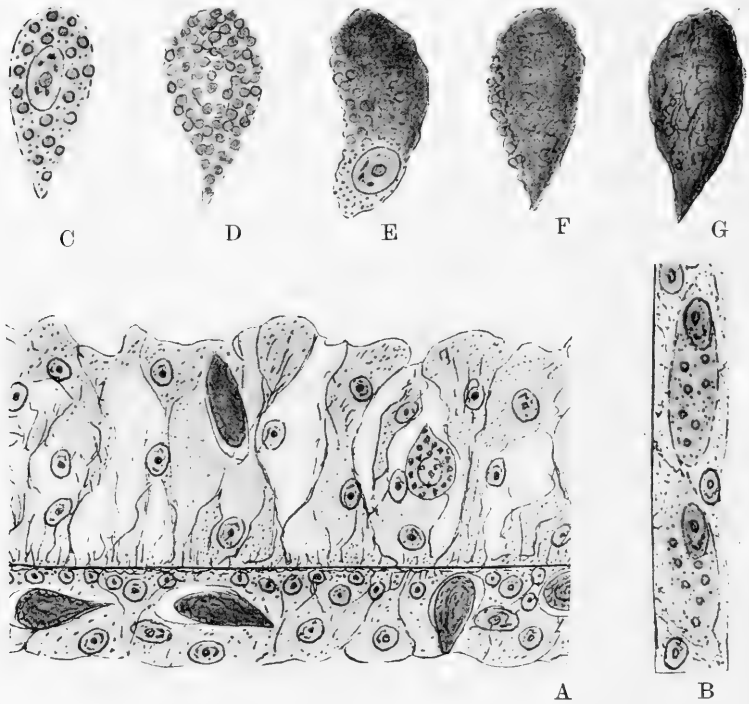
Sertularia linealis Warren. $\times 2000$.

as in fig. E, the nucleus may remain in a comparatively unaltered condition in a portion of the undifferentiated cytoplasm of the cell. The globules gradually fuse together and become much darker brown. In figs. E and F the fusion of the globules is seen to be taking place, the fusion being less complete on the left side than on the right. In fig. G the fusion is complete and the body consists of a more or less homogeneous substance of a dark brown colour and measures about $11\ \mu \times 4\ \mu$.

There is naturally considerable variation in the size and shape of the brown bodies, but there is a very obvious distinct tendency for them to possess a pear-shaped outline both in the ectoderm and endoderm. The bodies in the endoderm are often more elongated and larger than those in the ectoderm, but the difference between them is not as considerable as would be expected from the difference in the character of the

cells in the two layers. The brown bodies would appear to be dead, and an empty space often surrounds a considerable portion of a body (fig. A). Whether these spaces occur in the living tissue, resulting from the contracting away of the living

TEXT-FIG. 9.



Sertularia loculosa Busk. Fig. A, $\times 1150$. Fig. B, $\times 1900$.
Figs. C-G, $\times 2500$.

cytoplasm from the dead body, or whether they are shrinkage spaces arising during fixation, it is not possible to determine. There is no evidence that we are here dealing with a parasitic organism, or that the bodies are produced through the poisoning action of bacteria. The bodies in question appear to be undoubted transformations of hydroid protoplasm, resulting from untoward stimuli.

Black specimens of *Sertularia loculosa* are not uncommon, but they have not been found so frequently as specimens in the non-pigmented condition.

Paragattya intermedia Warren.

Text-figs. 10 and 11.

Here the black condition is not so common as in the species previously discussed, but it was found in material collected at Knysna and at Park Rynie, Natal.

The blackness is due to the presence of large, rounded, dark brown or black bodies in the ectoderm (text-fig. 10). These black bodies possess considerable depolarising power under crossed Nichols, while the pigment substances of the hydroids previously passed under review do not possess any appreciable influence on polarised light.

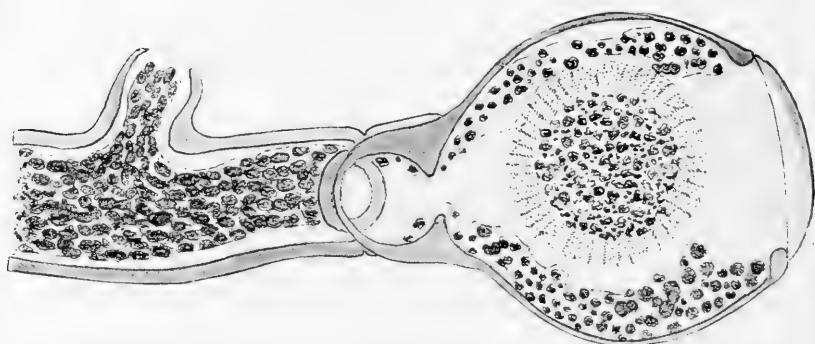
The normal ectoderm of *Paragattya intermedia* bears numerous large, oval or rounded cells which are charged with radiating elongated bodies of a homogeneous substance appearing to be of the nature of reserve food-material or yolk. In text-fig. 10 the cavity of the blastosphere of the developing planula may be seen to be filled tightly with these yolk-cells.

In text-fig. 11, E, normal yolk-cells are seen in surface view and in section lying in the ectoderm on the right-hand side of the figure, surrounded by interstitial cells and overlaid by large epithelial cells. In figs. A-D the growth of these cells is illustrated; A-C in optical section, D surface view.

The black bodies previously mentioned as giving rise to the black condition of certain specimens are derived from the transformation of yolk-cells. Under certain unfavourable stimuli the cells do not form normal yolk-bodies, but a coarse, granular condition of the cytoplasm arises, and the whole substance turns brown (fig. F). The coloration increases, and the cell may become very dark or black. The nucleus appears to swell (fig. G.). Ultimately the cell seems to die, and becomes converted into a rounded mass of homo-

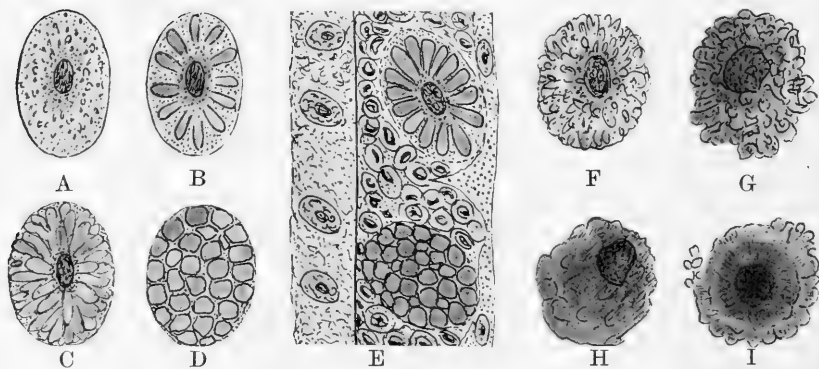
geneous dark brown substance (fig. 1). These transformed yolk-cells possess considerable depolarising power, and appear bright under crossed Nicols.

TEXT-FIG. 10.



Paragattya intermedia Warren. $\times 150$.

TEXT-FIG. 11.



Paragattya intermedia Warren. $\times 1100$.

In *Sertularia bidens* a single colony was found in which the living tissues had been almost entirely replaced by irregularly shaped, small, black bodies. The colony had succumbed, and it was not possible to learn anything about the histology of the pigmentation. Some sign of pigmentation

was noticed in the endoderm of *Kirchenpaueria mirabilis* (*Allman*), and a suggestion of the same was seen in *Sertularia acanthostoma* *Bale*.

COMPARATIVE REVIEW AND CONCLUSIONS.

In the present paper there has been described a number of examples of cellular degeneration in the tissues of certain hydroids, resulting in a general black or dark brown coloration of the entire colony. Only calyptoblastic hydroids have been found to be thus affected; but probably this is purely accidental, owing to the fact that the available material of gymnoblastic species is mostly sparse.

The cause or causes of this pigment-degeneration in the tissues have not been definitely ascertained; but bacteria or other parasites do not appear to be present, and there is some evidence for suspecting that intense insolation, especially when acting on an old colony, is at least one of the causes, if not the primary cause.

The cellular degeneration involves different cells and tissues in the various species of hydroids examined, and there is, so to speak, a specific kind of degeneration in each species. The degeneration processes lead to the formation of black or dark brown granules of characteristic shape and appearance and attaining to a more or less definite maximum size, and the cells, clusters of cells, or portions of cells, producing the granules tend to assume a characteristic shape and aspect. It would be quite easy to name the hydroid by an examination of the degenerated areas. Sometimes in place of the occurrence of discrete pigment granules, moderately large homogeneous masses of dark brown or black substance arise by the fusion of the granules, and these masses may tend to have a characteristic shape and size.

Microchemical tests indicate that the coloured granules or masses which are formed are of a proteid nature. Under the microscope the granules sometimes have the appearance of small globules of coloured fat, but osmic acid has no particular

action on them. The granules or masses vary considerably in the intensity of coloration, and a study of numerous sections leads to the view that the first products of degeneration of the living protoplasm consist of pale or nearly colourless granules of a proteid nature and of a mucilaginous, somewhat refringent, clear substance in which the granules lie embedded like cocci in a zooglea-matrix. Gradually the granules become coloured dark brown or black by a further decomposition, and a general coloration of the colony results therefrom. The protoplasm involved in the degeneration processes is gradually transformed into these products, and if the whole of the cell is thus transformed the cell dies. The nucleus sometimes swells, as described in the case of ganglion cells of an animal killed by sunstroke, and the chromatin is dissolved. Usually the conspicuous nucleolus persists unaltered after the chromatin has disappeared, but ultimately even this can be no longer found.

In *Lytocarpus filamentosus* (text-figs. 1-3), the cells of both the ectoderm and endoderm are similarly affected. The individual cells become converted into oval masses of dark brown granules or globules. The average size of the masses is about $25\mu \times 9\mu$, and the diameter of the largest granules is about 0.7μ . The death of the colony, or portion of a colony, does not occur until a very large number of the cells become involved. Contiguous cells may be affected, and a coarse reticulum of degenerated tissue may be formed in the ectoderm and endoderm.

In *Thuiaria tubuliformis* (text-figs. 4 and 5) pigment-degeneration occurs in both the ectoderm and the endoderm. In the case of the endoderm, a cluster of cells becomes affected, and an oval, chambered structure with pigmented walls arises. A frequent size is about $45\mu \times 30\mu$. Sometimes the structure is greatly elongated (e.g. 0.2 mm.) in the long axis of the cœnosarc-tube. The ectoderm cells may become swollen and erupted by the formation of cavities; but typically there is no very conspicuous swelling or coarse vacuolation of the protoplasm in the ectoderm. In the

ordinary ectoderm, pigmented streaks about $40\mu \times 7\mu$ are common. These are frequently bluntly rounded at one end and tapering at the other. The pigment granules are small, reaching about 0.4μ in diameter; but the pigment is not always present as discrete particles. Frequently it occurs as a lining to the cavities of the pigmented structure, and in the endoderm there are usually several masses of pigment of rounded or irregular shape lying in the cavities. Often in the ectoderm, and especially in the thin outer sheets of ectoderm, branching and very elongated streaks arise; these stretch through the epithelial cells and do not necessarily involve the whole of the cytoplasm of the individual cells through which the streaks pass.

In *Sertularia operculata* (text-fig. 6) pigmented chambered structures, similar to those in *Thuiaria tubuliformis*, occur in the endoderm. In the case of the ectoderm the diseased condition appears to lead to hypertrophy, resulting in undue multiplication of the interstitial cells, and the nuclei are in abnormal condition with their staining capacity considerably reduced. Small clusters of these interstitial cells run together, vacuolation of the protoplasm occurs and oval chambers are formed with the walls crowded with large pigment granules (figs. E-G), consisting of little dark brown or black discs (diameter about 1.0μ) and rodlets (length about 1.3μ). The discs and rodlets mimic cocci and bacteria in an extraordinary manner; but these bodies seem undoubtedly to arise from the transformation of the protoplasm of the hydroid.

The diseased condition of pigmentation may become very acute, and may lead to constriction and ultimate transverse division of the cœnosarc. The constriction would appear to result from the hypertrophy of the interstitial cells of the ectoderm.

In *Sertularella mediterranea* (text-fig. 7) the pigmented oval bodies, measuring about $17\mu \times 8\mu$, mostly correspond to separate cells. The bodies are not black but greenish-brown, and mimic unicellular algæ. As a matter of fact, unicellular algæ have been described as occurring in

abundance in the tissues of certain Siphonophora, but I have had no opportunity to compare them with the bodies found occasionally in *S. mediterranea*. There is no evidence, however, that the present bodies are really foreign organisms. The greenish globules are gradually formed in the cytoplasm of what appears to be a tissue cell of the hydroid (text-fig. 7, c). It is true that, in whatever tissue the bodies may arise, there is a tendency for them to assume the same oval shape and approximately the same size, but a like tendency has been noticed in other cases where the bodies do not mimic foreign organisms (cf. *Sertularia loculosa*). At times in the ectoderm there is a marked hypertrophy of the cells affected (text-fig. 7, B). The globules (about 0.4μ in diameter) are produced gradually in the cytoplasm, and the cell usually assumes an oval shape. Ultimately the cell becomes densely crowded with the globules and the chromatin of the nucleus is dissolved. Sometimes the bodies are rounded, and the granules fuse together and form a dead, brown mass (text-fig. 7, M).

In *Sertularia linealis* Warren (text-fig. 8) the interstitial cells of the ectoderm are affected in clusters, and chambered structures with blackened walls are formed, resembling those found in the endoderm of *Thuiaria tubuliformis* and *Sertularia operculata*.

In *Sertularia loculosa* Busk (text-fig. 9) certain cells, both in the ectoderm and endoderm, become pear-shaped, and there are gradually produced in the cytoplasm colourless globules of considerable size (about 0.8μ in diameter). The nucleus clarifies owing to the solution of the chromatin. Later, these globules become brown, fuse together, and form a dead, homogeneous and characteristic mass (about $11\mu \times 4\mu$) of yellowish-brown colour (fig. G). No trace of nucleus remains.

In *Paragattya intermedia* Warren (text-figs. 10 and 11) the pigmentation consists entirely in the blackening of reserve food cells or yolk-cells which occur in the ectoderm among the interstitial cells. No well-defined globules or pigment

granules are formed. The young yolk-cell, instead of producing normal yolk-masses, becomes coarsely heterogeneous in texture and gradually assumes a dark brown or black coloration. The nucleus swells and becomes indistinguishable, and the whole mass (measuring $15\ \mu \times 11\ \mu$) may subsequently become compact and homogeneous. A fully-formed yolk-cell with radial masses of yolk may sometimes degenerate in a similar manner. The degenerated cells may fuse together in twos or threes, and the whole colony becomes intensely black, and, doubtless, perishes (see text-fig. 10 where the planula and coenosarc are moribund). The yolk-masses have a weak depolarising power, but on browning and fusing together, to form a more or less homogeneous body, this power is greatly increased.

The yolk-cells are surrounded by many interstitial cells, but it is not easy to decide whether hypertrophy of this tissue, by an increase in the number of the cells, really accompanies the pigmentation of the yolk-cells. It will be remembered that in *Sertularia operculata* such hypertrophy appears to occur, but in that species the ordinary interstitial cells themselves become pigmented.

From this comparative review of the various examples of hydroid pigmentation we learn that there is a specific reaction of the tissues to certain unfavourable stimuli, and these reactions differ in the various species. It may be noted that marked differences occur among allied species of the same genus (cf. *Sertularia operculata*, *loculosa*, *linealis*). Thus, as known from experiments with immunity, physiological differences do not necessarily run exactly parallel to morphological differences, and there has arisen the conception of physiological species within a single morphological species. The same principle is seen in the well-known fact that two species of a genus, which morphologically are widely separate from each other, may be capable of crossing; while, on the other hand, two species which may be very closely similar to one another from a morphological standpoint, may be quite unable to cross.

The characteristic aspect of the degenerated areas must be

the result of an unseen architecture in the cytoplasm, which is only rendered visible by the physiological disturbance induced by the adverse stimuli. In many animal diseases such a disturbance may arise through the presence of toxins produced by parasitic bacteria, etc., which may be far distant from the actual place where cellular degeneration is occurring and eruptions and sores of characteristic appearance and shape are being formed. Nevertheless, characteristic diseases are not necessarily due to such poisons. Unfavourable stimuli of various nature, such as excessive heat, chemical rays of light, friction, undue pressure, etc., may produce a characteristic reaction in the protoplasm of the cells, and degeneration changes may set in and result in the production of visible effects, such as hyperpigmented spots, freckles, running sores, etc., entailing the death of cell-elements.

Degeneration changes may be confined to a particular portion of a cell, as is seen in text-fig. 6, H, where a symmetrically placed pigmented chamber occurs in each of two contiguous endoderm cells. Also, in text-fig. 4, A, C, may be seen the formation of branching streaks of degenerated protoplasm extending through portions of the living cytoplasm of a considerable number of cells which are in contact with one another. Here is evidence of the unseen architecture of the cell, referred to above, since the affected portions of the cytoplasm of the cell must be in a different physiological or physical condition from the other portions of the cytoplasm which are not so affected.

It is interesting to note the differences in the reactions which occur in the different species of hydroids when acted upon by what are presumably the same adverse stimuli; different kinds of cells may be affected and the characteristic shape and general facies of the degenerated areas differ to some extent in every species examined.

The reaction to these stimuli appears to be a definite one for each species, and does not seem to vary from time to time, although the individuals affected cannot always be in the

same physiological condition with regard to age, nutrition, reproduction, etc.

The production of new formations, to use a medical term, under the influence of adverse stimuli does not appear to be a marked feature associated with pigment-degeneration in hydroids; but in the case of *Sertularia operculata* there seems to be a distinct hypertrophy of the interstitial tissue resulting from an increase in the number of the rounded cells. The nuclei of these cells are peculiar in not readily staining with dyes and there may be no obvious nucleolus. The ectoderm is rendered remarkably thick and the myo-epithelial cells are mostly separated from the mesoglea, and appear as a somewhat flat epithelium of large cells with conspicuous nuclei near the surface. The ectoderm sheet around the hydranth is also hypertrophied (text-fig. 6, A). The constriction of the cœnosarc is probably connected with the multiplication of the interstitial cells, and the pigmentation of these cells constitutes the essential feature of the phenomenon in this hydroid. We have seen above that hypertrophy of the individual cells affected frequently occurs in that they may attain a size greater than the normal cell appropriate to the kind of tissue of which they form a part (text-fig. 4, F; text-fig. 7, B, interstitial ectoderm cells).

The action of intense light in inducing, or at any rate accelerating, the diseases, pellagra, Kaposi's disease (*Xeroderma pigmentosum*), and chloasma, and in the production of freckles and of the general pigmentation of the skin is well recognised. It is of interest to obtain evidence of an analogous reaction in simple organisms. Curiously enough, in the case of chloasma, different types of the pigmentation of the skin in patches are recognised, corresponding to the influences which undoubtedly must act energetically on hydroids occurring in exposed rock-pools between the tide-marks of the tropics; these are¹:

(1) *Chloasma solare* (*Melasma solare*) due to exposure to the sun or any powerful light such as reflection from

¹ Castellani and Chalmers, 'Manual of Tropical Medicine,' 2nd edit., London, 1913, p. 1612.

snow. In the case of the hydroids the reaction may be expected to be greater on tropical or sub-tropical coasts than elsewhere.

(2) *Chloasma caloricum* due to exposure to heat. In small isolated rock-pools exposed to the blaze of a tropical sun the water may become extremely warm and even fatally so when the tide has receded, and the barrenness of some of the pools may be partly attributed to this cause.

(3) *Chloasma traumaticum* resulting from mechanical irritation, paralleled by the agitation of the water beating the hydroid against the rocks or other objects.

(4) *Chloasma toxicum* resulting from irritating poisons. Certain rock-pools near the high-water mark are not filled at every high-tide. In these the water soon becomes stale and will have a prejudicial influence on the majority of the inhabitants, and, as a matter of fact, very few kinds of hydroids are capable of living in such pools.

These physical causes are not, however, the only ones which lead to diseased pigmentation in the higher animals, since the toxins in the blood resulting from syphilis, leprosy, tuberculosis, diabetes, etc., may induce hyperpigmentation in the skin. Also in so-called "pigmentary fever," which is supposed to be due to insolation, a pigmentation of the face occurs, and after the fever has left, it gradually fades away in the course of several months.

A closer study of the histology of the pigmented tissue resulting from disease in the higher animals would be of the greatest interest to compare with that of the blackened hydroids, and there is no doubt that observations on the pathology of simple organisms is capable of giving an important insight into the fundamental causes and effects of diseases as found in man and other mammals.

EXPLANATION OF PLATE XII,

Illustrating Dr. E. Warren's paper, "Observations on Cellular Degeneration and the Formation of Pigment in certain Hydroids."

Lytocarpus filamentosus (Lam.).

FIG. 1.— $\times 60$. Photo-micrograph of two pinnae in a normal unpigmented condition.

FIG. 2.— $\times 60$. A pinna in a strongly pigmented state; the tissues appear to be moribund.

FIG. 3.— $\times 60$. A pigmented pinna with the tissues disintegrating.

Thuiaria tubuliformis (M.-Turn.).

FIG. 4.— $\times 40$. Photo-micrograph of a portion of main stem showing the commencement of pigmentation in the cœnosarc. Note the leopard-like spots.

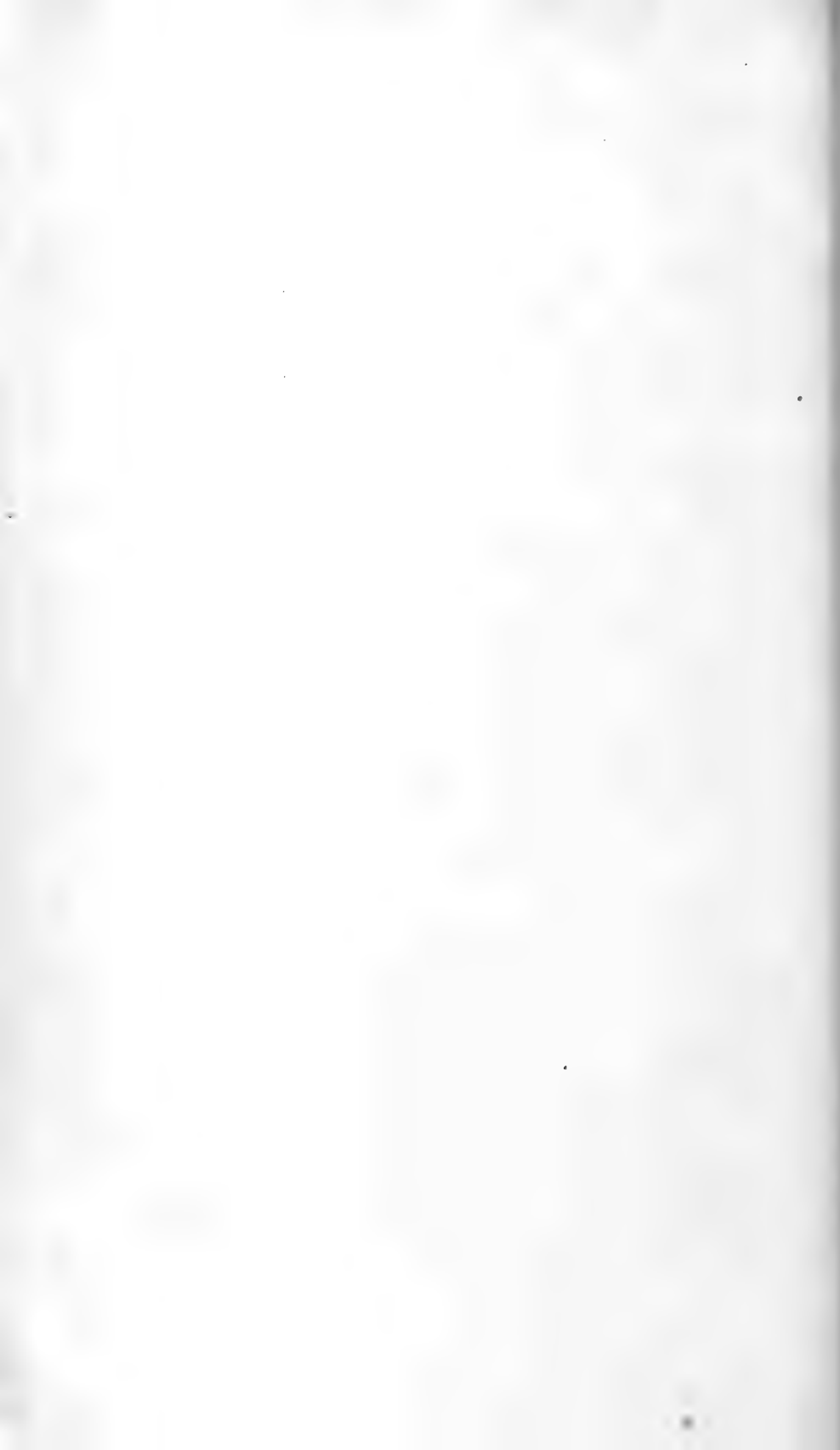
FIG. 5.— $\times 40$. Specimen in an advanced stage of pigment-degeneration.

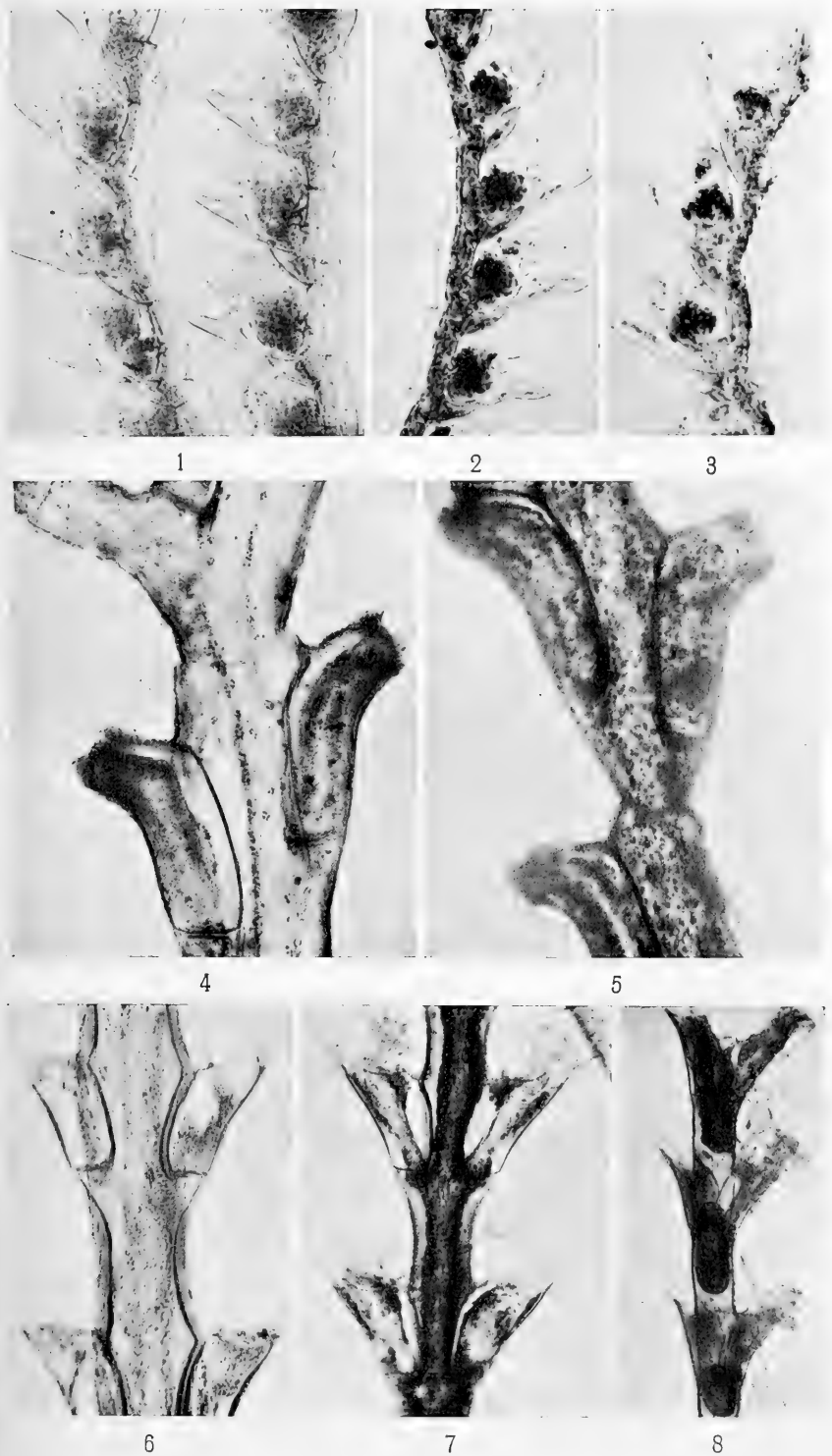
Sertularia operculata Linn.

FIG. 6.— $\times 40$. Photo-micrograph of a portion of a branch in an unpigmented condition.

FIG. 7.— $\times 40$. Branch strongly pigmented, but the hydranths are still alive with distended tentacles.

FIG. 8.— $\times 40$. Branch in an advanced stage of pigmentation. The cœnosarc has divided transversely in three places, but the hydranths are alive and the tentacles are expanded.





LYTOCARPUS FILAMENTOSUS (*Lam.*). Figs. 1-3, $\times 60$.
 THUIARIA TUBULIFORMIS (*M.-Turn.*). Figs. 4, 5, $\times 40$.
 SERTULARIA OPERCULATA, *Linn.* Figs. 6-8, $\times 40$.

**South African Bagworms; a New Sub-genus and
Species of the Genus *Acanthopsyche*, and
a Re-description of *Trichocossus arvensis*
Janse.**

By

A. J. T. Janse, F.E.S.L.

With 1 Text-figure.

Genus *ACANTHOPSYCHE* *Heyl*.

Subgenus nov. *SEMIMANATHA*.

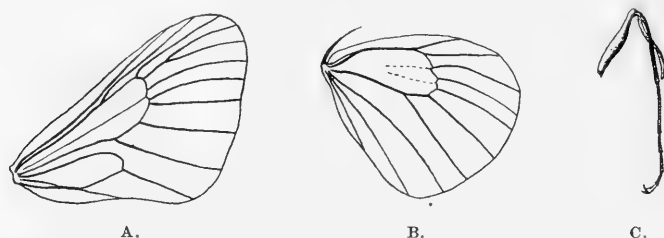
Type *fumosa* sp. n.

Fore tibiae with a long thin process, as long as the tibia; palpi minute; tongue absent; antennae a little over one-third of costa, bipectinate, branches from base to beyond middle as long as one-third of whole antenna, each branch with rather long cilia on both sides and some branches ending in a bristle. Fore wing with 1c anastomosing with 1b at half; 1b forked at base and with a spur from one-fourth of 1b to inner margin at half; cell over half of wing; 2 from two-thirds lower median; 3 from five-sixths; 4 and 5 from lower angle, nearly from a point; 4 straight; 5 curved near origin; 6 from middle of disco-cellular, parallel to 5*; lower half of disco-

* Sir George Hampson in his key to the subgenera mentions the absence of vein 6 for some subgenera; judging from the position of the vein present in this subgenus I would say that 6 is here present and vein 7 absent; the space between that vein and vein 8 suggests also that the missing vein is 7.

cellular angled inwards below half, from where it emits a small veinlet into the cell; disco-cellular beyond 6 straight; 7 absent; 8 and 9 on a stalk of one-third and from upper angle of cell; 10 remote from stalk of 8, 9; 11 from upper median at two-thirds; upper median very much incurved at basal half; 12 parallel to upper median and the greater part of 11. Hind wing with cell a little over half of wing; lower median slightly incurved at one-third; upper median well excurved, parallel to costa; 2 from two-thirds lower median; 3 from two-thirds distance vein 2 to lower angle; disco-cellular very oblique inwardly, straight; 4 from lower angle; 5 from one-fourth disco-cellular, obviously but gently curved

TEXT-FIG. 1.



Semimanatha fumosa sp. n. Male.

- A. Fore wing showing venation. $\times 2$. B. Hind wing. $\times 2$.
C. Fore leg of male. $\times 4$.

in middle; 6 from one-half disco-cellular, curved at one-third; 7 from upper angle, gently curved upwards; a short veinlet into the cell just below 6; 8 free at basal third, then anastomosing with upper median for nearly whole length, then oblique to costa.

The shape of the fore wing is much more triangular than in any *Acanthopsyche* known to me; in fact, it is even more triangular than in *Manatha*, a subgenus which this one resembles very much in general aspect, but the presence of a distinct process on the fore tibiae prevents me from placing it in the genus *Psyche*. Perhaps this points to the insignificance of this character for a natural classification of this family.

Fore wing triangular; costa slightly hollow at one-third; apex well rounded; termen nearly straight, erect, slightly rounded at between 2 and 4; tornus well rounded; inner margin slightly lobed at one-third.

Hind wing triangular; costa arched; apex well-rounded; termen and tornus well-rounded; inner margin somewhat arched.

This subgenus comes perhaps nearest to *Brachycyttarus Hmps.*, but differs from it in the fore wing with a rather long cell, 4 and 5 being free, and the hind wing with 8 anastomosing with upper median instead of connected to it by a bar.

Semimanatha fumosa sp. n.

Male.—Head, thorax and abdomen on upper side thinly covered with olive-brown (XL) hairs; on under side with white hairs; shaft of antenna olive-brown, branches fuscous-black (XLVI); legs with femora and tibiæ covered with long olive-brown hairs, tarsi with tawny-olive (XXIX) hairs; fore wing and hind wing uniformly and rather densely covered with olive-brown hairs; costa of fore wing on upper and under side with a narrow black line reaching to apex; underside as above, but slightly lighter; cilia buffy-brown (XL) with basal third olive-brown.

Exp., 19 mm.

Hab.—Pietermaritzburg (Natal), bred by C. B. Hardenberg, emerged in December and January.

Three specimens in collection Janse: type December 18th, 1916; cotypes December 27th, 1916, and January 2nd, 1917 (the latter two with abdomens missing).

Trichocossus arvensis Janse.

Trichocossus arvensis Janse. Ann. Natal Mus., 1917, vol. iii, pt. 3, p. 613.

A revision of the original description is given below.

Male.—Head, thorax at the sides, abdomen, femora and

tibiae covered with long white hairs, shaft of antenna with white scales on upper side; thorax above with long glaucous-grey (XLVIII) hairs; palpi with chætura drab (XLVI) hairs; tarsi ringed with white.

Fore wing ground colour chætura drab; at base some long white hairs; hyaline patches and markings, thinly covered with white scales; a sub-basal series of irregular patches beginning at costa to near inner margin; a big rounded medial patch in cell and small round marks above and before it on costa; three similar marks below it, the middle one a little inwards; a light broad streak below lower median from sub-basal to medial patches; a post-medial series of broad rounded spots, first three confluent and from costa to vein 9, two near subterminal spots between veins 5 and 7, two more inwardly between 3 and 5 and two more outwardly between 1c and 3; a subterminal series of 7 rather smaller rounded spots between costa and vein 3; cilia white with a fuscous base.

Hind wing with the ground colour as in upper wing; a white area in cell and below it as far as 1c; beyond it a slight irregular light portion, which is diffusely covered with scales of ground colour suggesting a series of post-medial and sub-terminal confluent spots; inner marginal area covered with long white hairs; cilia as in upper wing. Under side as above, but markings less clearly defined and more confluent; on hind wing some additional subcostal white scaling on basal half and a similar post-medial patch near costa.

On account of the appearance of Mr. Hardenberg's papers on the life-histories of the bagworms I previously described this species in 1917 ('Ann. Natal Museum,' vol. iii, p. 613), from material which has now proved inadequate. Since then better specimens have been reared by Mr. Hardenberg and they all show the white markings distinctly. During flight these markings readily disappear, giving the specimen a rubbed appearance as mentioned in the original description. There is no doubt whatever that the specimen (New Hanover, February 3rd, 1917) described here is identical with the type

and cotype of *T. arvensis*. This specimen is also in my collection.

The following species should also be added to the list of South African Psychidæ:

Chalia Moore, A.M.H.N. (4), xx, p. 345 (1877).

Ch. maledicta Scheben, 'Arch. Schiff's Hyg.,' 14, p. 697 (1910).

To be placed after *Manatha*.



South African Bagworms: their Transformations, Life-history and Economic Importance.

PART II.

By

C. B. Hardenberg, M.A.,

Entomologist in Charge of Wattle Insect Investigations, Natal.

With Plate XIII and 25 Text-figures.

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2. *Acanthopsyche tristis* *Janse*. Pl. XIII, figs. 1-7.

The "Thatched Bagworm"—Fam. Psychidæ, Subfam.
Psychinæ.

Acanthopsyche (*Oeceticoides*) *tristis* *Janse*. Ann. Natal Mus.,
1917, vol. iii, pt. 3, p. 597.

This bagworm, while not uncommon, has apparently seldom
been observed, owing to its retiring habits. Although, judging

from the composition of its bag-covering, it presumably feeds on grasses, I have very rarely (one specimen only) noticed it in its supposedly natural surroundings, but have usually found the bags attached to tree-trunks, fence-posts, walls of buildings, projecting ledges of rocks, and fastened to various objects in rubbish-heaps ready for pupation. Larvæ actually feeding I have found only on the lower branches of the black wattle, *Acacia mollissima*, but this is certainly not its natural food-plant.

We therefore find practically no mention of this species in literature, and the moth had not been reared till 1915, when we succeeded in breeding some half-dozen males. The moth, proving to be new, has been described by Janse as *Acanthopsyche tristis*.

The only writer who has mentioned this species, so far as I can ascertain, is Claude Fuller, who in his article on "Some Natal Bagworms and Basket-worms," quoted in Pt. I, figured its bag and gave it the popular name of "The Wandering Bagworm," probably on account of its bag being usually found away from its food-plant, thus evidencing a tendency to travel on the part of the fully-grown larva. Junod, in his 'Faune Entomologique de Delagoa,' does not enumerate this species and does not figure its bag, so that it appears to be uncommon in that locality. Nevertheless it should occur there also, as isolated specimens have been found by the writer at Eshowe, Zululand, and by Janse at Durban. We have found it more frequently at higher altitudes, between two and four thousand feet.

Food-plants.—During the spring (October) of 1917 the writer found this species fairly abundantly in Pietermaritzburg on the foliage of *Asparagus*, and a few other ornamental plants. On the latter they were probably accidental feeders, but the *Asparagus* appeared to be eminently suitable for their development, and specimens in captivity were fed entirely on it with satisfactory results, the long slender petioles and twigs of the plant lending themselves very well to the construction of the bag-covering. Its distribution was very

local, i. e. only here and there I found a garden where the asparagus was being attacked, but where present the species proved fairly abundant, for as many as twenty specimens were taken from one small bush. The presence of old bags showed that the species had occurred on the same bush for several seasons.

An unchecked normal increase may make this species first a nuisance in the garden and ultimately a pest.

THE EGG.

The eggs have not been found, and we have no data relative to the duration of the egg-stage. The eggs, while in the body of the gravid female, measure 0.4 by 0.45 mm. They are deposited in the chrysalis shell of the female, mixed with hairs, scales, and, it seemed, also a considerable quantity of white silk.

The number of eggs laid by one female has not been determined, but, judging from the gravid female, must be considerable, as in the case of *A. junodi*.

LARVA, FIRST INSTAR.

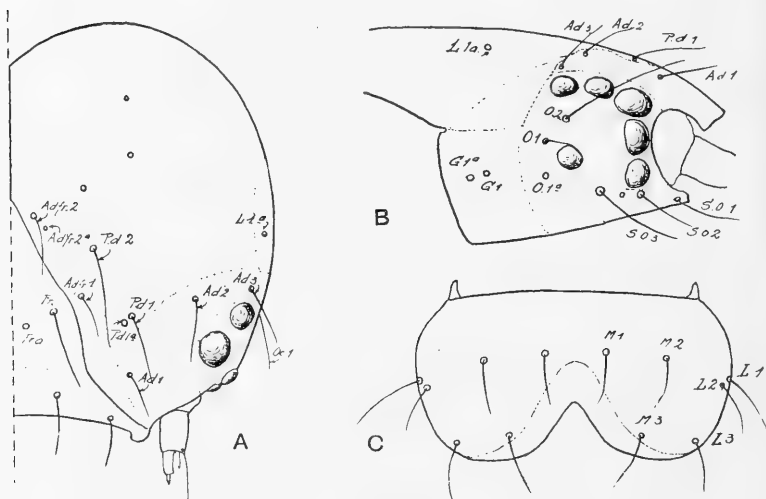
Length of larva 1.6 mm. Ground colour cream buff (XXX)*; head tawny (XV); thoracic plates, dorsal plate on 8th abdominal segment and suranal plate natal brown (XL); thoracic legs and hooks on prolegs fuscous (XLVI). The larva is somewhat lighter coloured than that of *A. junodi*, and does not show such a pronounced up-bending of the abdomen.

HEAD.—Width of head-case 0.43 mm., median epicranial cleft shallow. Frons large, reaching to half the total height of head. Adfrontals not separated from the epicrania, clypeus not separated from the frons. Head-capsule uniformly coloured, the future pattern faintly indicated by a slightly darker coloration.

* These numbers refer to Ridgway's 'Color Standards and Nomenclature,' edition 1912.

Setæ: Postero-dorsal Region.—The setæ¹ are all situated on the lower third of this region. Pd. 1 about level with frontal seta (text-fig. 1, A, B); puncture pd.1a medio-ventral and close to pd. 1; pd. 2 close to adfrontal region and about equidistant from adfr. 1 and adfr. 2. Puncture pd. 2 could not be found. The upper part of the postero-

TEXT-FIG. 1.



Acanthopsyche tristis Janse. Larva, first instar.

- A. Left side of head, with regions indicated and showing position of setæ. $\times 170$. B. Latero-ventral view of ocellar area, with regions indicated and showing position of setæ. $\times 170$. C. Labrum, showing position of setæ. $\times 170$.

dorsal region shows three secondary punctures, the median one a little higher than the top of the frons.

Antero-dorsal Region.—Seta ad. 1 close to adfr. region about level with the base of the frons; ad. 2 about level with

¹ In describing the distribution of the setæ the system of Dampf-Heinrich has been followed, as it simplifies their enumeration. Alfons Dampf, 'Zur Kenntniss gehäusetragender Lepidopteren-larven,' Königsberg i. Pr., 1910. Carl Heinrich, "On the Taxonomic Value of some Larval Characters in the Lepidoptera," 'Proceedings of the Entomological Society of Washington,' xviii, 3, pp. 154-164, September, 1916.

adfr. 1 and in line with adfr. 2 and pd. 2; ad. 3 latero-dorsal to ad. 2. No puncture ad. 2a could be seen.

Adfrontal Region.—Adfr. 1 close to and latero-dorsal to fr.; adfr. 2 near tip of frons.; puncture adfr. 2a close to seta adfr. 2.

Frontal Region.—Frontal punctures fr.a close to median line at about lower one-fourth of the frons; frontal seta fr. close to adfr. 1 and on a line connecting puncture fr.a and seta adfr. 1.

Clypeal, or Epipharyngeal Region.—Seta 1 close to distal edge and below pd. 2; seta 2 further away from distal edge and below seta fr.; the distance between 1 and 2 less than that between 1 on each side.

Ocellar Region.—Setæ o. 1 and o. 2 close together; o. 2 about half-way between the two hindmost ocelli. Puncture o. 1a rather distant from o. 1; seta o. 3 could not be found.

Subocellar Region.—Seta s.o. 1 at antero-median corner; s.o. 2 and s.o. 3 closely approximated; s.o. 2 just below lower ocellus; puncture s. o. 2a about half-way between s.o. 2 and s.o. 3

Gular Region.—Seta and puncture g. 1 and g. 1a close together, behind o. 1a.

Lateral Region.—Lateral seta l. 1 could not be found; only puncture l. 1a.

Labrum.—About twice as wide as high; median cleft one-third of total height. Setæ m. 1 and m. 2 about equidistant, m. 2 slightly lower than m. 1; m. 3 moved up to the edge of the epipharyngeal thickening and slightly medial to m. 2; l. 1 marginal, slightly lower than m. 2; l. 2 close to l. 1, medio-distal; l. 3 submarginal, slightly lateral to m. 2 (text-fig. 1, c).

Mandibles.—Subquadrate, five-toothed, second tooth the largest and with a slight step on each side. Outer three teeth sharp, inner two blunt, the fifth almost rudimentary.

Labium and maxillæ show no distinctive peculiarities.

THORAX AND ABDOMEN.—Position of setæ does not show any important differences from that described for *A. junodi*,



but the setæ themselves are more conspicuous, and, especially the medio-dorsal ones, much longer. The number of hooks on the abdominal prolegs are, as usual, not constant, though approximately half of the number to be acquired at later instars. They range from 10 to 12; those on the anal prolegs are 8 in number.

The numbers on the single specimen examined were as follows:

Side.	Abd. 3.	Abd. 4.	Abd. 5.	Abd. 6.	Anal.
Right .	11	10	10	10	8
Left .	12	12	12	11	8

The claws on the thoracic legs have a finger-like, fleshy projection at the base of the teeth.

Intermediate instars not fully known. No differences from from the full-grown larva, except in size, were noticed.

LARVA, FULL-GROWN.

Length 24 mm. (full-grown female). Width of head-case 3 mm. Ground colour of body maize yellow (IV). Dorsal aspect of abdominal segments vinaceous slate (L), passing medially into anthracin purple (XLIV). Anterior half of abd. segments 3 to 8 mineral red (XXVII). Pattern on head, dorsal plates on thorax and abd. segments aniline black (L); the ground colour of these plates maize yellow (IV) diffused with apricot orange (XIV).

HEAD.—Width of head-case 3 mm. Pattern on head as shown in text-fig. 3.

Postero-dorsal Region.—Setæ congregated on lower fourth, pd. 1 about level with adfr. 1 and above ad. 1; pd. 2 about level with adfrontal puncture, slightly above line connecting pd. 1 and adfr. 2, a little nearer to the latter. No puncture pd. 2a could be found (text-fig. 2, A).

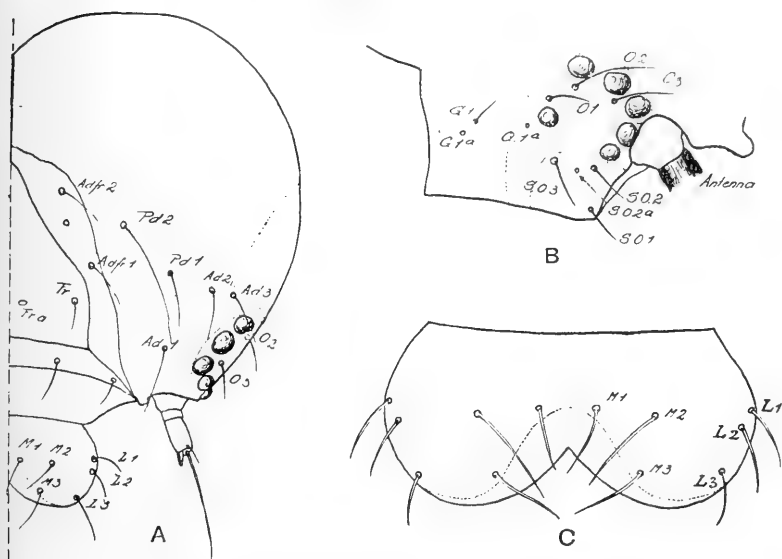
Antero-dorsal Region.—Ad. 1 below pd. 1 and about

level with lower edge of frons ; ad. 2 and ad. 3 close together, placed a little lower than adfr. 1.

Adfrontal Region.—Adfrontals massive ; adfr. 1 higher than fr. ; adfr. 2 below top of frons ; puncture adfr. a little nearer to adfr. 2 than to adfr. 1.

Frontal Region.—Frons large, equilateral, reaching to

TEXT-FIG. 2.



Acanthopsyche tristis Janse. Larva, full grown.

- A. Left side of head, showing regions and their setæ. $\times 27$.
 B. Latero-ventral aspect of ocellar region, showing setæ. $\times 27$.
 C. Labrum, showing setæ. $\times 27$.

two-thirds of the total height of the epicrania. Frontal punctures at lower one-fifth of frons, close to median line. Frontal setæ far apart, slightly above punctures.

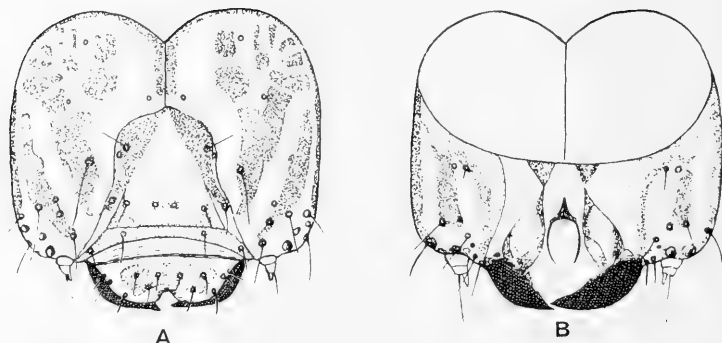
Clypeal Region.—Setæ 1 and 2 closer together than the distance between 1 of each side.

Ocellar Region.—Arrangement of setæ as in text-fig. 2, B. Puncture o. 1a almost directly below o. 1.

Sub-ocular Region.—Setæ s.o. 2 and s.o. 3 fairly close



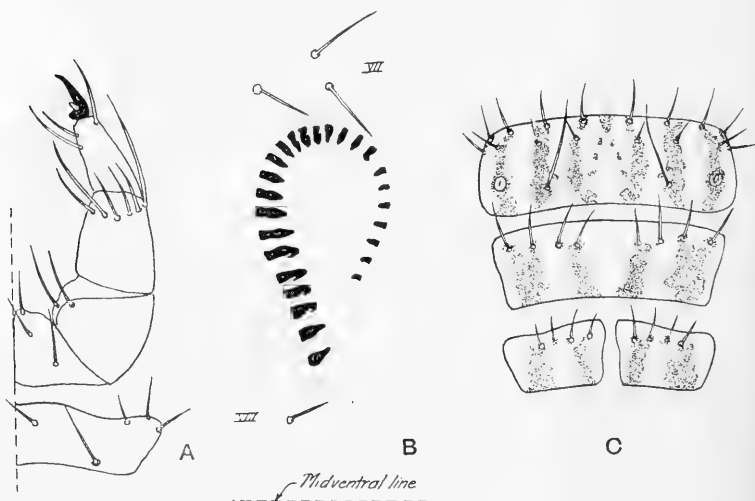
TEXT-FIG. 3.



Acanthopsyche tristis Janse. Adult larva.

- A. Front view of head, showing colour-pattern and position of setae. $\times 14$. B. Ventral view of head-capsule, showing colour-pattern and setae; labial parts are not shown. $\times 14$.

TEXT-FIG. 4.



Acanthopsyche tristis Janse. Larva, full grown.

- A. Prothoracic leg, showing lobe at base of claw and arrangement of setae. $\times 20$. B. Arrangement of hooks on left proleg of fourth abdominal segment. $\times 80$. C. Dorsal shields of thoracic segments, showing colour-pattern and setae. $\times 11$.

together, with s.o. 2*a* slightly medial to a line connecting the two, and nearer to s.o. 2 than to s.o. 3.

Gular Region.—Seta g. 1 short, almost straight behind o. 1*a*; puncture g. 1*a* medio-caudal to g. 1.

Labrum.—About twice as wide as high, median notch extending up to one-third of the total height. M. 1 and m. 2 closer than m. 2 and l. 2; m. 3 moved up till within the edge of the hypopharyngeal thickening. L. 1 slightly higher than m. 1; l. 2 close to, and medio-distal to, l. 1, submarginal; l. 3 moved inward from the margin (text-fig. 2, c).

Thorax and Abdomen.—Thoracic plates with pattern as shown in text-fig. 4, c. Position of setæ on thorax and abdomen similar to that described for *A. junodi*. The setiferous plates on the abdominal segments are rather conspicuous, and the 1st abd. shows a rather large dorsal shield resembling that of the thoracic segments. On the following segment we find the posterior tubercles fused into one transverse ridge, the anterior ones separate. All these segments are strongly wrinkled on the dorsal aspect, this wrinkled area being considerably darker than the lateral and ventral parts. On the 8th abdominal segment we find again a broad dorsal shield, while the suranal plate is large, covering the entire dorsal aspect of the 10th segment.

The number of proleg hooks (text-fig. 4, b) varies slightly as shown in the table:

Segment.	1.		2.	
	Right.	Left.	Right.	Left.
Abd. 3 .	22	25	24	23
Abd. 4 .	28	27	20	23
Abd. 5 .	28	30	18	23
Abd. 6 .	25	27	27	26
Anal .	22	22	19	16

Tristis has also a prepupal light-coloured instar, like *A. junodi* and *C. moddermanni*. Larvæ were found in this instar on November 24th. The colour is different from that of *A. alba* or *Gymnelema vinctus* in the corresponding instar.

Length 17 mm., width of head-case 2 mm. Ground colour of larva chamois (XXX). Head olive-buff (XL), apparently without markings. The markings on thoracic shields and on 8th to 10th abdominal segments olive-brown (XL). Spiracles cinnamon-rufous (XIV).

The spiracles on the first two abdominal segments are larger than those on the following segments, 3 to 7. The spiracles on the abdominal segments are placed transversely, that on the prothorax longitudinally.

HABITS OF THE LARVA.

Immediately upon leaving the bag in which hatching occurs the young start making a miniature bag. For this purpose they use the silk and small pieces of débris from the old mother-bag. This first shelter is made before any feeding is done, and, in fact, no part of the food-plant is used in its construction. We removed a young larva which had only just made for itself a circlet behind the thorax, put it with some wattle-leaf in a glass tube which was plugged with cotton-wool. The larva left the wattle-leaf and crawled up to the top of the tube, where it utilised strands of the cotton-wool to complete its bag. The process of making this first bag occupied between two and three hours. Only after this bag had been made did the larva start to feed on the wattle-leaf supplied, and it then used small particles of this to make additions to its bag.

During this first stage the larvæ are positively phototropic, like those of *A. junodi*, the instinct being developed in connection with dispersal. Later on, especially towards the time of pupation, they show a tendency to conceal themselves, as

the old bags are always found in shady and protected places, as mentioned above.

Dispersal is effected by the wind as the primary agent. The young larvæ, when ready to abandon the parent bag, presumably crawl about until they are in a position where the wind can pick them up. Only then do they begin to spin a long thread of silk in the same manner as the larvæ of *A. junodi*, and are thus carried about, while animals and birds may play a subsidiary rôle in this process of dispersal.

The Bags.—The bag of the full-grown larva is about 40 to 45 mm., consisting of a long, oval case of silk, mixed with small particles of leaf and stem, and covered with long blades of grass or long, narrow strips of midrib and other parts of the leaf of the food-plant. These are arranged lengthwise, but attached to the bag only at one end—the anterior end of the bag. Here they are fastened for a short distance, as far as the larva can reach without leaving its bag, the remainder of the stick projecting at a tangent. Several rows of these furnish the covering, and as each succeeding one covers the anterior part of its predecessor, the entire covering resembles a thatched surface, suggesting the popular name of the "Thatched bagworm" (Pl. XIII, figs. 1-7).

Food-plants and Economic Importance.—From the construction of the majority of the bags which we have been able to collect we must conclude that the natural food of this species is furnished by various grasses. But specimens have also been found feeding on the wattle, while Mr. Bell-Marley, of Durban, mentions that it feeds on "pomegranate and other shrubs." When on the wattle it was invariably found feeding on the lower branches, so that it is essentially a low herbage feeder; but as we have seen bags made up entirely of wattle leaves, it may in time develop into a wattle feeder and then become injurious.

THE PUPA.

When pupation time approaches the larvæ show a tendency to become gregarious, in so far as they all seek a place of

concealment, and thus several may be found together in such places. No exact data are at hand relating to the length of the pupa stage, but in our laboratory a male specimen, which had fastened its bag to the top of the breeding-cage during the fourth week in November, emerged on January 9th, so that the length of the pupa stage is at least six weeks.

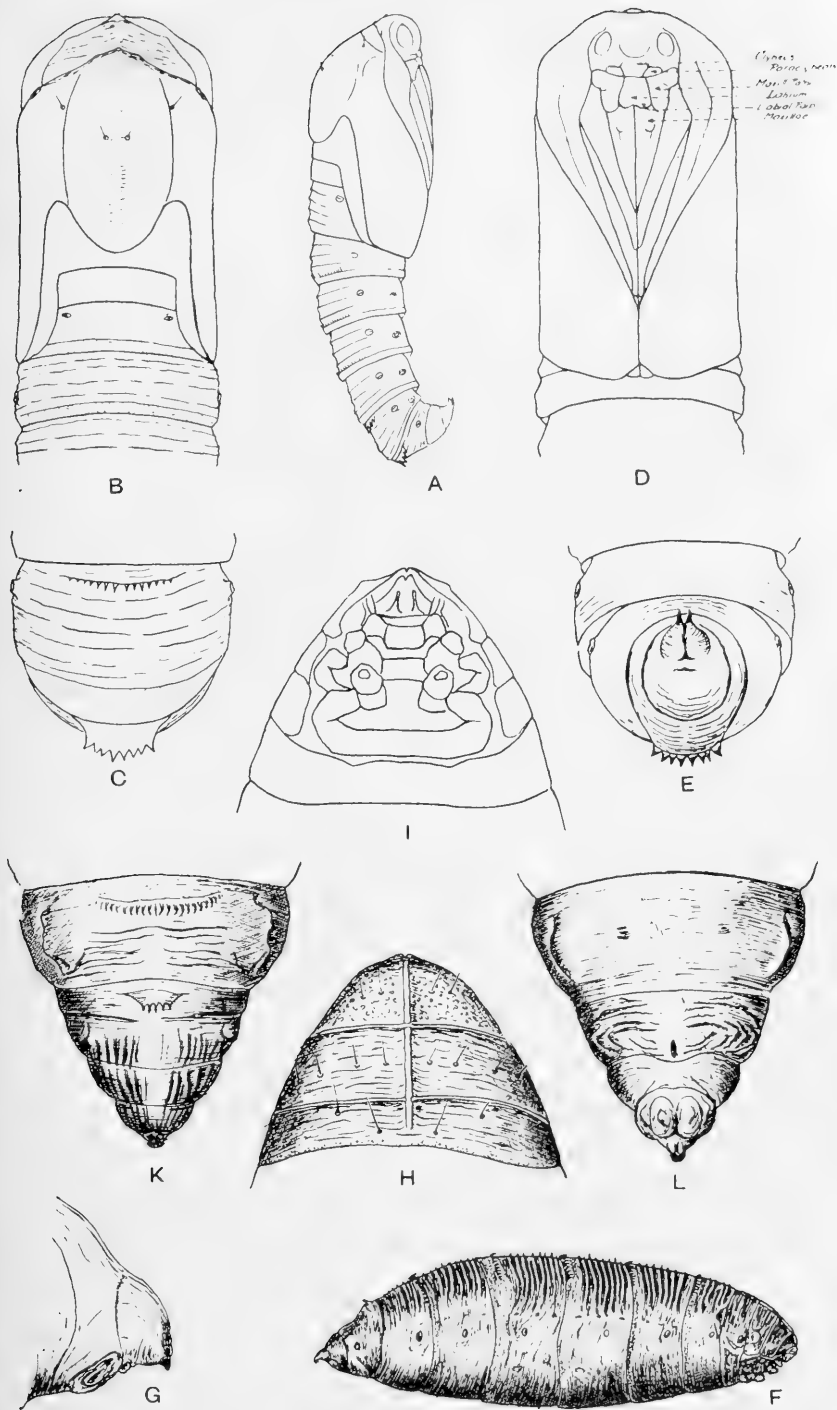
No inner bag is made, such as is found in *A. junodi*; but the larva turns around in its bag, and the space between the chrysalis and the wall of the case is filled with loosely woven, white, fluffy silk, which is more voluminous in the case of the female and extends down the neck of the bag. When pupating, the lower part of the bag of the female is filled with a comparatively loose mass of pure white, sticky silk, this material also filling to a less extent the space between the sides of the pupa and the wall of the bag. When the female has emerged we find the lower portion yellowish buff in colour, and the strands of silk of which it is composed covered with small scales. The yellow colour is probably derived from some fluid exuded by the emerging female, which filters down through the white silk, while the scales are rubbed off from her body.

Male Pupa.—Length 12 mm., width $3\frac{1}{2}$ mm. at mesothorax. General colour of thorax and wing-cases Hay's russet (XIV), abdominal segments burnt sienna (II), vertex of head antimony yellow (XV). Head, thorax, and appendages shiny; abdomen matte. Head slightly projecting ventrally, vertex broadly rounded. Antenna-cases broadened at base, gradually tapering toward the tip, reaching nearly to the end of the mesothoracic legs. Antennæ transversely striate to the

TEXT-FIG. 5.—*Acanthopsyche tristis* Janse. Pupa.

- A. Side view of male pupa. $\times 5$. B. Dorsal view of anterior part of male pupa. $\times 8$. C. Dorsal view of posterior part. $\times 8$. D. Ventral view of anterior part. $\times 8$. E. Ventral view of posterior part. $\times 8$. F. Lateral view of female pupa. $\times 3$. G. Side view of anterior end of female pupa. $\times 11$. H. Dorsal view of anterior part. $\times 10$. J. Ventral view of anterior part. $\times 10$. K. Dorsal view of posterior part. $\times 10$. L. Ventral view of posterior part. $\times 10$.

TEXT-FIG. 5.



tip, shallowly sulcate along the stem for about half its length (text-fig. 5, A-E). Clypeus small, trapezoidal, paraclypeals large, transverse, distinct. Labium large, labial palpi short, rounded. Maxillary palpi large, triangular, subdivided so as to show two lobes. Maxillae prominent, reaching to half the distance from labium to top of 2nd legs.

Pronotum transversely striate, anterior edge bisulcate, ending in a short median point. Mesonotum large, very convex dorsally, anterior edge sulcate, angular in median third, wing-cases reaching to posterior edge of 2nd abdominal segment. Metanotum narrow, lateral anterior angles high, narrowly rounded; hind wings visible to posterior edge of fore wings.

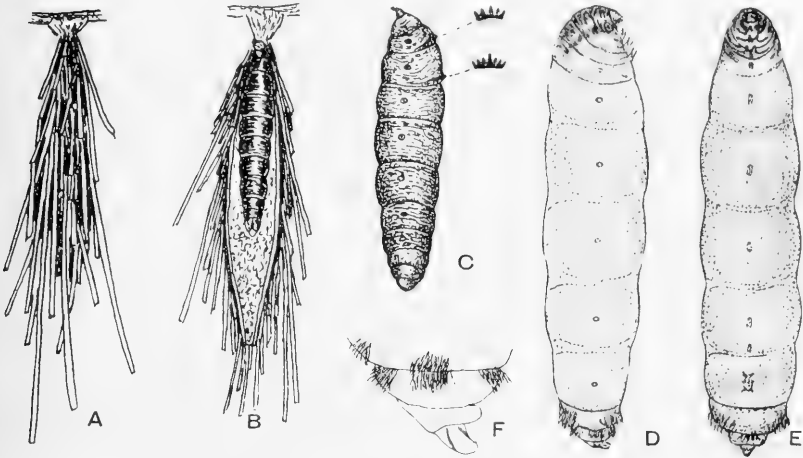
Abdomen as a whole deflected ventrally, especially the 7th and following segments. Dorsal aspect of abdominal segments strongly transversely ridged, ventral surface smooth. Posterior edge of 3rd to 5th segments with a dorsal row of minute hooks, directed forwards; 7th and 8th with a crescent-shaped transverse ridge at their cephalic edge, which ridge bears a row of stronger hooks, pointed posteriorly. Those on the 8th segment are the largest and are eight in number. Cremaster armature consists of two short, curved, slightly divergent prongs on broad, convex base, flattened laterally and directed ventrally.

Female Pupa.—Length 19 mm., thickness 5 mm., vermiform. Greatest thickness at 4th and 5th abdominal segments, and from there the pupa tapers gradually towards both ends (text-fig. 5, F-L). Colour chestnut.

Head with its entire aspect facing ventrally, concealed under the prothorax, very much wrinkled. Clypeus quadrate, paraclypeals small but distinct. Thoracic segments and the first abdominal with a dorsal median carina, which does not extend quite to the caudal edge of the first abdominal segment. Dorsal aspect of these segments transversely striate, that of the following segments 2 to 6 strongly transversely wrinkled; abd. 7 striate, abd. 8, 9 and 10 longitudinally striate. Abd. 2 to 5 with a row of fine recurved teeth on

posterior edge, largest and best developed on abd. 2. Abd. 6 without any teeth, abd. 7 with a short row on anterior edge. Abd. 8 with a short, transverse carina bearing five rather blunt teeth; abd. 9 and 10 bear no dorsal armature (text-fig. 6, c). On the lateral aspect we find that on the thoracic segments there is a membranous space between the pronotum and the prosternum. On the abdominal segments the

TEXT-FIG. 6.



Acanthopsyche tristis Janse.

- A. Bag of female. $\times 1.25$. B. Opened bag of female, showing pupa within. $\times 1.25$. C. Female pupa. $\times 2$. D. Side view of female. $\times 3.5$. E. Ventral view of female. $\times 3.5$. F. Side view of posterior end of female. $\times 10$.

transverse sulci of the dorsal aspect become striæ on the lateral region. Position of spiracles lateral, not protruding, that on the 8th abdominal not noticeably larger nor more dorsally placed than those on the other segments.

On the ventral aspect we find the thoracic leg-cases present as broad median plates with short stumpy projections. Ventral aspect of abdominal segments finely striate. The cremaster consists of a conical base bearing two minute, slightly divergent hooks.

THE IMAGO.

Only the male is winged. It is a dull grey moth, with a sprinkling of black hairs over the wings, thicker at the basal half, so that the outer part of the wings looks transparent. The moth is small, expanding only some 20 mm., and is of rather slow flight. We have seen it flying just at dusk, but it is not attracted to the light (Pl. XIII, fig. 7).

The female is of the usual Psychid type, wingless. As the female appears to be unknown, a description of the only specimen bred is given.

Adult Female.—Female apterous, vermiform. Length 17 mm.; width and depth $4\frac{1}{2}$ mm. at 6th abdominal segment, tapering gradually from there cephalad, more abruptly caudad. Body wall transparent, its colour maize yellow (IV). The head is chitinous, as also the first thoracic segment on its dorsal and lateral aspect; the following two thoracic segments and the anterior half of the first abdominal segment are chitinised on their dorsal aspect only. These chitinised parts are Mars yellow (III) shading into amber brown (III). Head small, conical, broadly rounded in front, directed ventro-caudad, with small eye-spots and a median orifice. Prothoracic spiracle large, prominent, those on the other segments hardly distinguishable.

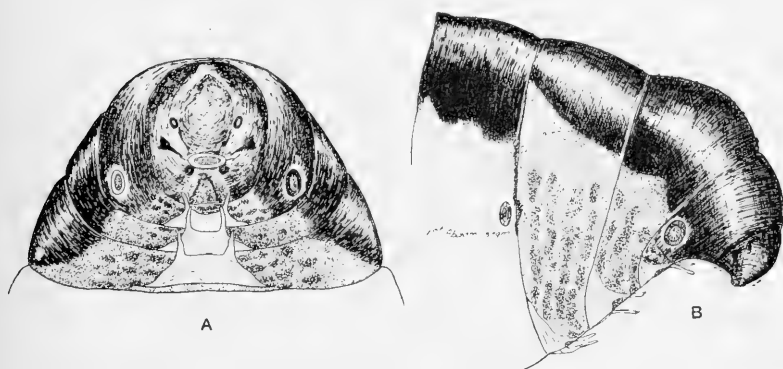
Legs vestigial, represented by a thin, bifurcate, transverse plats on each of the thoracic segments (text-fig. 7, A, B). The legs show a considerable variation in the amount of their development. While in some specimens they are represented only by membranous appendages, in other cases they show a fair amount of chitinisation; they are fused in the median line to a much smaller extent, are no longer flat, show a certain thickness, and the coxal parts can be distinguished from a distal portion. In no instances, however, could the presence of terminal claws be ascertained.

Body wall transparent, so much so that the eggs contained in the body are distinctly visible and the nerve ganglia can be plainly seen on the ventral aspect. Abdominal segment 7

with a small supra- and infra-spiracular tuft of hairy scales, of raw sienna (III). Abd. 8 with large prominent dorsal and lateral tuft of antique brown (III) scaly hairs (text-fig. 6, D, E). Abd. 9 with a thin chitinous band at anterior edge, extending along the ventral and lateral aspect. Ovipositor supported by a mid-dorsal chitinous rod, dividing anteriorly into two concave branches, and two smaller, subventral ones.

Female normally enclosed in chrysalis shell, only the head, thorax and part of the 1st abdominal segment exposed.

TEXT-FIG. 7.



Acanthopsyche tristis Janse. Female.

A. Ventral view of anterior part of adult female, showing head and rudimentary thoracic legs. $\times 20$. B. Side view of same, showing legs and the chitinisations of the thoracic and first abdominal segments. $\times 20$.

New Hanover, Natal, February 1st, 1915. Bred by C. B. Hardenberg, one specimen.

SEASONAL HISTORY AND NUMBER OF GENERATIONS.

Adult moths were found at the end of November and as late as the beginning of February. While this suggests the occurrence of two generations a year, it is more probable that we have here merely a long flight-period, as we saw also in *A. junodi*. Mr. Bell-Marley informs me (in lit.) that he had a larva feeding for eight months, the moth at last

appearing on November 25th. We collected on August 21st a more than half-grown larva; it fed up to the latter part of November, and the imago appeared in January. We can thus safely assume that there is only one generation in a year, and the moths appear throughout the summer.

At present the species is of no economic importance. We have observed only a few specimens, and have not noticed any serious damage arising from their presence. The species is small and of slow growth, and therefore the plant would have a chance to out-grow any injury due to loss of foliage, unless the bagworms occurred in great numbers.

From the half-dozen specimens or so which we have had an opportunity to breed no parasites have been obtained.

3. *Acanthopsyche alba* Janse. Pl. XIII, fig. 8.

Acanthopsyche (Metisa) *alba* Janse. Ann. Natal Mus., 1917, vol. iii, pt. 3, p. 598.

This species is of about the same size as the Wattle Bagworm, *A. junodi*, Heylaerts. It has not yet been found in numbers in the Wattle plantations inland. While not entirely confined to the coast, since we have found it as far inland as Pietermaritzburg, it seems to thrive better in the coastal area. There it may be found locally common at times on the thorn trees; but it has very seldom been bred or captured, and it was described only last year by Janse from a male specimen obtained at Nkweleni, Zululand. The species is very difficult to rear, for even in the later stages, when most of the other bagworm species are not so very particular about the kind of food which is offered to them, this insect objects strongly to any change, and refuses to eat even when transferred from the common thorn tree (*Acacia* sp.) to a tree so nearly related as the Black Wattle (*Acacia mollissima*). Out of some fifty specimens collected in a later stage of larval life, not a single one reached maturity. Mr. E. E. Platt, of Durban, succeeded in rearing a few males from a similar lot.

The various stages of the larval life of this bagworm are

as yet very imperfectly known, and some careful breeding remains to be done to fill up the gaps.

Systematic Position.—The species belongs to the family Psychidæ, sub-fam. Psychinæ, and was described by Janse (loc. cit.) under the name of *Acanthopsyche alba*. The type was captured at light—a very unusual occurrence—and it is the only species of this group which I have ever noticed to fly so late as to come under the influence of light attraction.

The type and other specimens known to Janse were males; the female has not been described.

Food-plants.—"The larva feeds on acacia or wattle or both" (E. E. Platt, in lit.). Mr. Platt and the writer found the species abundant on a thorn tree (*Acacia* sp.) near the Race-course at Durban, and I also found it attached to the trunk of an *Eucalyptus* in Mr. Todd's garden at Phœnix, Natal. In the latter case there were no native acacias near, but the garden was surrounded by wattle plantations, and as it is very improbable that the bagworm feeds on *Eucalyptus*, we must infer that it had fed on the surrounding wattles. However, in captivity the specimens obtained from the thorn tree at Durban refused to eat wattle leaves; neither did the first instar larvæ take to them. We may therefore conclude that the species is very particular about its food-plant, and an individual larva, or group of larvæ from the same brood, does not readily make a change. On the other hand, there are probably some races which have adapted themselves to wattle and other plants, and a brood probably chooses only those food-plants on which the parents thrive. This lack of adaptability on the part of the young larva may explain the relative scarcity of the species.

Of other food-plants the following may be mentioned: in October, 1917, the writer found isolated specimens, practically full-grown, on *Cupressus macrocarpa* and on privet (*Ligustrum vulgare*), both commonly used for hedges. In neither case was there any leguminous tree or shrub in the immediate neighbourhood from which the larvæ might have

wandered. In fact, the specimen found on the macrocarpa actually had a piece of the leaf of this plant attached to its bag, indicating that it had been feeding on it.

The writer also found the species feeding on *Stigma-phyllon ciliatum* (Fam. Malpighiaceæ) in the garden of the Natal Museum; while Dr. C. Akerman collected a specimen from a rose-bush in Pietermaritzburg. This bag had been fastened for pupation, and contained a living pupa.

LARVA, FIRST INSTAR.

Upon hatching the larva is about 1 mm. long, when fully stretched 1.5 mm., uniformly olive buff (XL) in colour, with the head, legs, and dorsal chitinous plates on the 1st to 3rd thoracic and 8th to 10th abdominal segments olive brown (XL); claws on thoracic legs and hooks on prolegs natal brown (XL).

Of the chitinous dorsal plates that on the 1st thoracic segment is the largest, extending over the entire width of the segment, that on the 2nd is somewhat narrower, while that on the 3rd occupies only the anterior half and is interrupted in the middle. The abdominal segments following the thorax are free from chitinous plates, while these again appear on the 8th abdominal segment, increasing in size and extent to the 10th segment, where the anal plate occupies the entire dorsum of the segment.

The position of the setæ agrees with that of *A. junodi*, previously discussed, and the number of hooklets on the anal prolegs average 10 in number (text-fig. 8, D); on the abdominal prolegs they may reach the number 12, as shown in the table on p. 163.

Here, also, only half the normal number of hooklets are present during the first instar of the larva.

The young larvæ made their first bag out of material gnawed off the parent bag, this first bag being about 1.5 mm. in length and 0.75 mm. in width. It is wide, and either truncated or somewhat barrel-shaped.

Unfortunately the larvæ would not feed in captivity, and we have no data on the length of the various instars.

Segment.	1.		2.		3.		4.	
	Right.	Left.	Right.	Left.	Right.	Left.	Right.	Left.
Abd. 3 .	10	11	9	10	11	12	10	10
Abd. 4 .	10	10	10	9	11	11	11	12
Abd. 5 .	10	10	10	10	12	12	10	10
Abd. 6 .	11	9	10	11	11	11	11	8
Anal .	10	9	10	10	11	10	10	10

LARVA, FULL-GROWN.

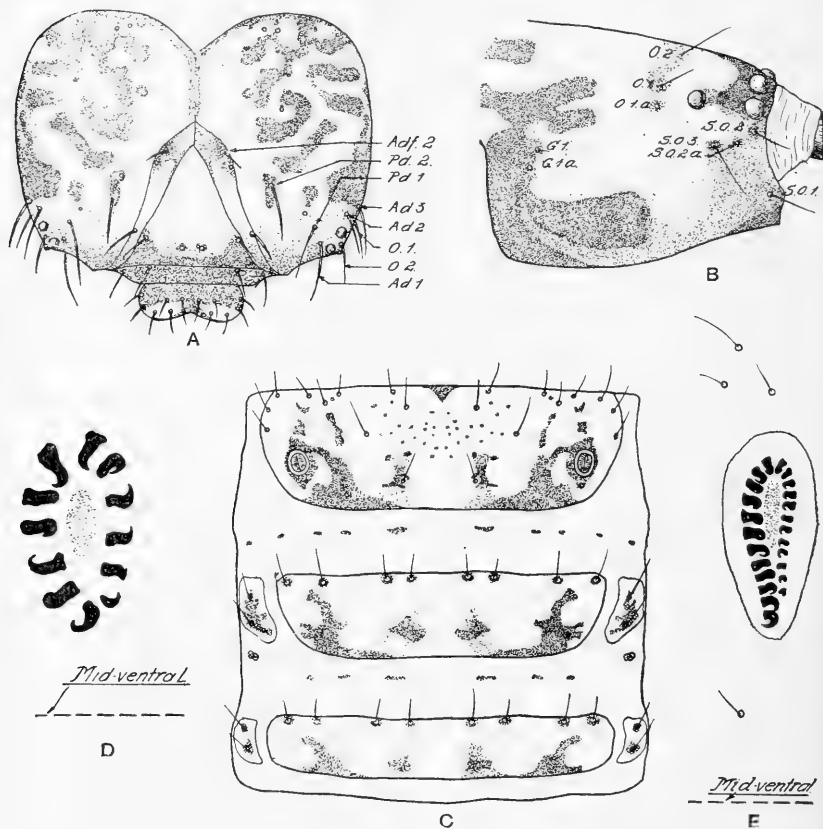
Length 18 mm. (male), 25 mm. (female). Width of head-case 20 to 30 mm. in the full-grown male larva; in the female it may reach a width of 40 mm. Ground colour of head avellaneous (XL), of dorsal thoracic plates olive buff (XL), of body pale drab grey (XLVI). Dorsal area and ventral area of abdominal segments, also the thoracic intersegmental membranes, drab (XLVI), markings on head, thoracic plates and plates on 8th to 10th abdominal segments hair brown (XL). Spiracles cinnamon buff (XXIX).

The thoracic plates show very little pigmentation as compared with the other *Acanthopsyche* larvæ, and the specific name *alba* is also borne out by the aspect of the caterpillar as well as that of the adult. The longitudinal pigmented stripes, so prominent in *A. junodi*, are reduced to short lines on the posterior half of the thoracic plates as shown in text-fig. 8, c. The setæ are placed in the position normal for this family and have been discussed under *A. junodi*. The intersegmental membranes are characterised by a series of small pigmented areas arranged in transverse rows, while a rudimentary spiracle is found between the 2nd and 3rd thoracic segments.

The larva is typically *Psychid*, the head has a radial colour-pattern, the adfrontals are massive, the head setæ are

congregated at the lower half of the epicrania (text-fig. 8, A, B), the thoracic legs increase in size from the 1st to the 3rd

TEXT-FIG. 8.



Acanthopsyche alba Janse. Larva, full grown (except D).

- A. Antero-dorsal view of head, showing pattern and arrangement of setae; mouth parts, except labrum, not shown. $\times 11$. B. Postero-ventral view of ocellar and subocellar region, showing pattern and setae. $\times 34$. C. Dorsal view of thoracic plates. $\times 6$. D. Number and arrangement of hooklets on abdominal proleg of first instar larva. $\times 56$. E. Hooklets on abdominal proleg of full-grown larva. $\times 28$.

pair, the hooklets on the abdominal prolegs are arranged in a single loop, open at the medio-caudal aspect, the hooks of

the anterior half of the loop well-developed and those on the posterior half rudimentary, or rather decreasing in size towards the middle line (text-fig. 8, E). Number of hooklets on the abdominal legs range from 22 to 30, those on the anal legs from 16 (probably abnormal) to 25, the average number being 22. The hooklets have a strong base, with long, pointed ends, strongly curved.

The Bags.—The bag is more or less pear-shaped, not more than four-sided, tapering gradually to a long point at the lower end and not abruptly rounded at the upper end (Pl. XIII, fig. 8). It consists of an inner silken, long, oval case, to the outside of which are attached short pieces of thorns and twigs. These are affixed transversely and attached in the middle, the ends projecting free, and have the bark gnawed off at the place of attachment. In the case of the twigs being hollow the eaten-off portion extends so deep as to expose the cavity of the stick. Probably the gnawed-off material is mixed with the silk of the bag to make a thorough union. Over these twigs there is spun another layer of silk, enveloping them almost entirely, leaving only the tips exposed. The entire structure looks as if it were some object which had been entangled in a spider's web and had been spun over by the spider, and as such it is probably well protected against predaceous enemies and parasites. This becomes the more probable, as from a batch of about fifty bags of early mature larvæ we have not obtained a single parasite, while in some other species of bagworms, living in the open, the number of parasitised individuals amounted to from 40 to 60 per cent.

The bag of the mature female reaches a length of from 30 to 45 mm.; the male bags are somewhat smaller, their maximum length not exceeding 35 mm.

THE PUPA.

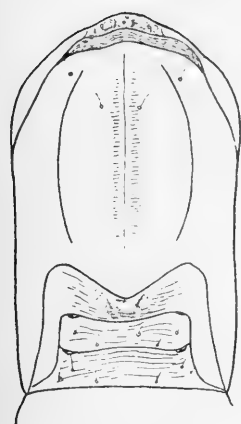
Male Pupa.—Length 12 mm. General colour chestnut (II), wing-cases, declivities of abdominal segments carob-brown (XIV). Surface shiny.

Head: Vertex broadly rounded with transverse carina at anterior extremity, the part of vertex dorso-caudal of this region rugose, remainder faintly punctulate. Clypeus small, transverse; paraclypeals round triangular. Labium broadened and bilobed distally. Maxillæ broad, maxillary palpi large, trapezoidal, divided into a medio-caudal and latero-cephalic part. Antennæ broad for the first half and reaching to the tip of the first leg-cases, deeply sulcate longitudinally for two-thirds of their length, transversely striate over their entire length. Second leg-cases reaching only to just below the first leg-cases. Wing-cases extending ventrally to half the width of the 3rd abdominal segment. Pronotum with anterior edge sinuate, surface rugose. Mesonotum large, anterior third sharply declivous, posterior two-thirds straight, sub-parallel to the ventral side, with a fine median longitudinal groove, surface finely transversely striate. Humeral angles broad, rectangular, hind edge of wing-cases straight, dorso-lateral angle only slightly rounded. Metanotum short, striato-punctulate; hind wing-cases broadly visible to the posterior edge of the second abdominal segment (text-fig. 9, A, C, E). Abdominal segments on dorsal aspect transversely striate, shiny; posterior declivities matte, granulate, broadly visible from 2nd to 8th segment. Segments 3 to 5 bear a row of minute teeth on this caudal declivity, with long, spine-like setæ, directed anteriorly; abd. 6, 7 and 8 have in addition a crescent-shaped plate near the anterior margin, armed with strong spines directed posteriorly; these reach their greatest development on the 7th segment. On the ventro-lateral and lateral aspects the abdominal segments are smooth and unarmed. Segment 10 has a cremaster apparatus,

TEXT-FIG. 9.—*Acanthopsyche alba* Janse.

- A. Dorsal view of anterior part of male pupa. $\times 7$. B. Dorsal view of posterior part of male pupa. $\times 7$. C. Ventral view of anterior part of male pupa. $\times 7$. D. Ventral view of posterior part of male pupa. $\times 7$. E. Side view of male pupa. $\times 4$. F. Dorsal view of female pupa. $\times 3.3$. G. Ventral view of female pupa. $\times 3.3$. H. Ventral view of posterior end of female pupa. $\times 5$. I. Ventral view of anterior end of female pupa. $\times 17$. K. Side view of female pupa. $\times 3.3$.

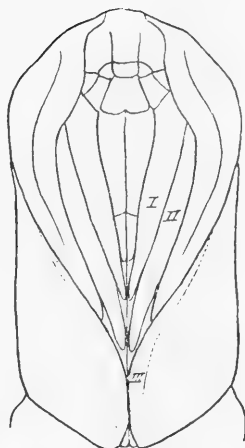
TEXT-FIG. 9.



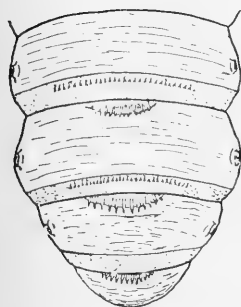
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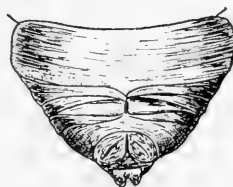
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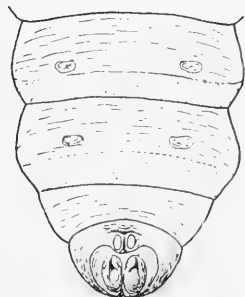
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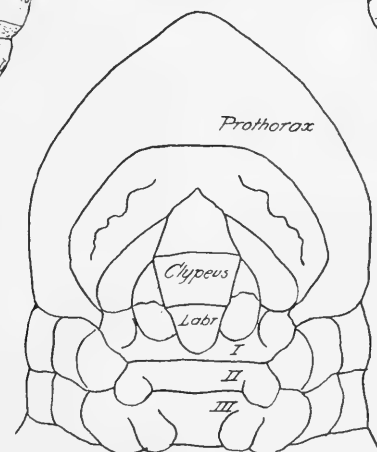
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H



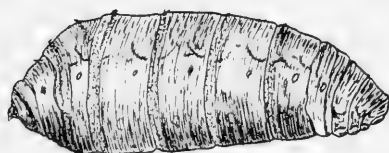
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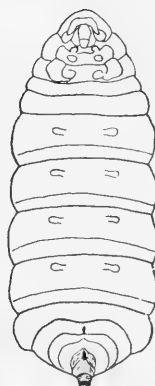
I



F



K



G

consisting of two parallel spines on conical bases, flattened laterally and directed posteriorly (text-fig. 9, B, D).

Female Pupa.—Length 17 mm., width 6 mm. at end of 6th abdominal segment, subcylindrical from 3rd to 6th abdominal segment; from the 3rd it gradually tapers to the head, from the 6th it is more abruptly rounded to the caudal end. Colour mahogany red (II), head parts and thoracic segments liver-brown (XIV).

Head concealed under prothorax, excessively rugose so as to obscure the parts of which it is composed. Clypeus large, paraclypeals and maxillary palpi distinct. Prothorax projected over the head, ventral aspect with flat median crest, surface of prothorax strongly rugose. Prothoracic leg-cases small, consisting of a narrow median part ending in two hemispherical clubs, directly posteriorly. Leg-cases not detached. Meso- and metathorax with larger leg-cases, directed posteriorly and extending the entire width of the segments (text-fig. 9, F, G, I). First abdominal segment narrow; succeeding segments increase in width till the 6th; smooth, shiny, finely striatulate transversely; posterior declivities punctulate, matte. Seventh segment longitudinally striate; 8th smooth, with small genital scar; 9th and 10th finely sulcate transversely. Dorsal aspect: thoracic segments coarsely rugose, abdominal segments finely transversely striate, abd. 3 to 6 with a short transverse row of minute spines, directed anteriorly; 6 and 7 with a short transverse row of spines directed posteriorly, which have become vestigial on the 8th segment and are here represented by a median pair of small spines only; 9th segment unarmed; 10th segment with a cremaster apparatus consisting of a broad, transverse, quadrate plate, appearing to be the fusion of four spines directed ventrally (text-fig. 9, H, K).

THE IMAGO.

Emergence.—When the female is ready to receive the male the pupa-case splits on the dorsal side by a median

fissure which reaches to the posterior edge of the metathorax, and by a transverse suture from the vertex along what corresponds to the posterior edge of the antennal cases down as far as the posterior edge of the metathorax. The anterior part of the pupa thus comes off in three roughly triangular pieces, the pieces breaking off transversely along the inter-segmental incisions. Through the slits thus formed we find extending a ribbon of strongly woven silk, which reaches down through the neck of the bag. This ribbon is cream-coloured, the threads appear to be cemented together, and it is quite distinct from the mass of loosely woven, white, fluffy silk which fills the remainder of the neck of the bag and the space around the chrysalis. It is absent in the bags containing male pupæ, and therefore it would appear to have some sexual significance.

When the male moth is ready to emerge the pupa splits behind the head, around the back of the antennal and leg-cases, and a median split occurs down the prothorax and mesothorax. The male pupa protrudes from the bag as far as the end of the 5th abdominal segment, and usually at an angle.

Male.—The male moth is of about the size of that of *A. junodi*, but it has the thorax and abdomen covered with white hairs. The wings are transparent, with a dark line along the costa.

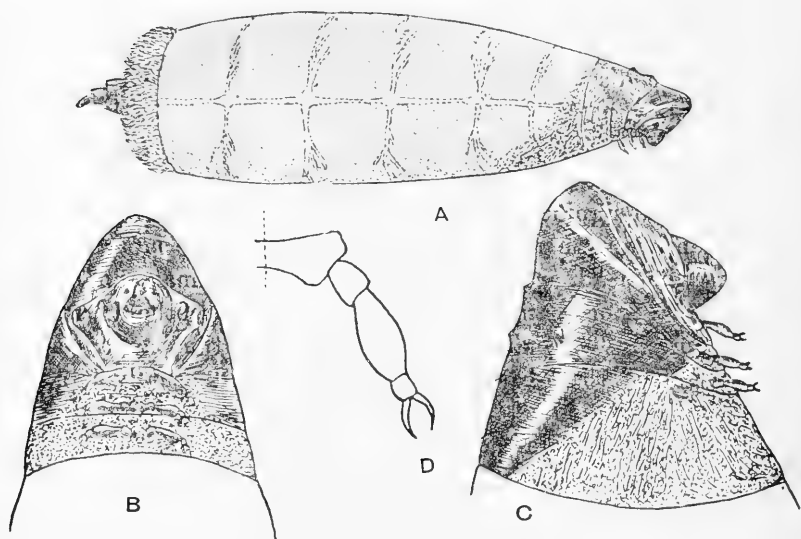
Female.—A description of the female is here given of the one specimen reared at New Hanover from Durban material, since it has not been previously described.

Length 20 mm., body cylindrical, tapering from the 4th abdominal segment towards the head, abruptly truncated at posterior end from the 7th and 8th abdominal segments. Colour of body pale dull green-yellow (XVII), ventral side of 3rd abdominal segment diffused with deep slaty brown (L), especially at the sides, which colour becomes more general and intensified on the ventral and lateral aspects of the 2nd and 1st abdominal and the 3rd thoracic segments. Posterior abd. segments 7 and 8 densely covered with matted hairs,



maize yellow (IV). Abd. segment 9 narrow, tubular, cinnamon brown (XV), with fine silky pubescence; its dorsal aspect strengthened by two lateral ridges, high at their cephalic end, tapering down to a point at the caudal end. Abd. 10 annular, Dresden brown (XV), finely plurisetose. Ovipositor ochraceous tawny (XV), truncated conical, its dorsal aspect strengthened

TEXT-FIG. 10.



Acanthopsyche alba Jause.

- A. Side view of female. $\times 4$. B. Ventral view of anterior part of female. $\times 15$. C. Side view of anterior part of female. $\times 15$. D. One of the thoracic legs, showing its considerable development. $\times 75$.

by two lateral, short, triangular ridges. End of ovipositor deflected ventrally.

Head small, rounded conical, deflected ventrally, entirely concealed underneath the prothorax (text-fig. 10, A, B, C). Vertex slightly setose laterally, and with a minute median sulcus. Prothorax small, its dorsal half deflexed, facing anteriorly, finely and sparsely setose on its lateral and dorsal

aspect. Prothoracic spiracle prominent, protected by a strong ridge, running latero-anteriorly from the insertion of the legs. Mesothorax broad dorsally, its anterior dorsal third deflexed, its lateral aspect sparsely and finely setose. Metathorax with a sharp median ridge, and laterally to this, a minute spine. Dorsal and dorso-lateral aspect of thoracic segments and of 1st abdominal segment chitinised, shiny. Prothorax entirely chitinised, but more strongly on its dorsal half.

Thoracic segments bear free legs, coxæ and femora short, tibiæ swollen in the middle, tarsi uni-jointed with two short, stout claws (text-fig. 10, D).

Behaviour of the Adults.—We have not bred the male moths, and at present no information is available on the subject of flight, copulation, length of life, etc. Mr. Platt reports that the males which emerged in confinement quickly battered themselves. It appears, therefore that they fly soon after emergence, and are strong flyers.

As the type has been captured at light in Zululand, it is probable that the emergence takes place at dusk and that the male flight is either nocturnal or crepuscular.

Number of Generations in a Season.—Judging from the emergences of the moth, there must be a considerable irregularity in the production of broods. The dates of emergence of specimens bred by Mr. Platt and the writer are as follows:

September 2nd, 1916, 1 male; November 5th, 1 male; November 9th, 1 male, 1 female; November 28th, 2 females; December 2nd, 1 male (E. E. Platt, Durban); December 10th, 1 male (C. B. Hardenberg, New Hanover); January 10th, 1916 (type, collected by Janse, Zululand).

If we had the records of only the first and the last date of flight we should be tempted to consider this species as two-brooded, since these dates correspond with those of other moths which have two generations; but the intermediate dates show that there can be only one generation in a season. The adults dated from September 2nd till December 10th were all obtained from one lot of caterpillars collected on one

individual tree, and which, when gathered, appeared to be of about the same size and age.

Geographical Distribution.—Until recently, the species seemed to be confined to places at or near the Natal Coast, judging from the localities on record; but during the spring of 1917 the writer found a few isolated specimens at Pietermaritzburg.

The localities whence the species has been recorded thus far are the following: Nkwaleni, Zululand (Janse, the type); Durban, Natal (Platt, Hardenberg); Phoenix, Natal (Hardenberg); Pietermaritzburg (Akerman, Hardenberg).

Economic Importance.—For the present the species cannot be considered sufficiently abundant to cause any apprehension. Its potentiality for injury is, of course, as great as that of the Wattle Bagworm, *A. junodi*, and the more so as the species appears to be practically free from parasitic enemies. Given especially favourable conditions for its increase, it may become a pest to be reckoned with, for it may be mentioned that while collecting these bagworms at Durban we found over a hundred on one thorn tree, which was stripped by them.

From the variety of food-plants above mentioned, it appears that this species is in the transition stage, a few individuals adapting themselves to plants other than acacia, and it is probable that this species, before becoming a menace to the large plantations, will first make itself felt as a nuisance in the garden on various ornamental plants.

4. *Clania moddermanni* (Heylaerts). Pl. XIII, figs. 9–14.

Eumeta moddermanni Heyl. Ann. Soc. Ent. Belg., 1888, vol. xxii, p. lix; Kirby, Cat. i, p. 503.

Clania moddermanni (Heyl.). Janse, Ann. Natal Mus., 1917, vol. iii, pt. 3, p. 592.

This is the largest species of bagworm which we have thus far found in South Africa. The bag is very characteristic, as can be seen from the photographs (Pl. XIII, figs. 9–14), and

has suggested to Fuller the popular name of "Lictor Bagworm." It was discussed under this name in his pamphlet on "Common Bagworms and Basket-worms" (Bull. XVI, Natal Department of Agriculture, 1909). In the same publication Fuller mentions and gives an illustration of another bagworm which he designated as the "Thorn Bagworm," but this has proved to be identical with the Lictor Bagworm now under discussion, the former being merely a Lictor Bagworm which had used the thorns of the native acacia in the formation of its bag. During a visit to Ladysmith in September, 1915, the writer found bags of this species on the thorn trees and also on various fruit trees, the latter being apparently part of the same infestation. While those on the fruit trees had made their bags of sticks, those on the thorn trees had constructed it either from thorns alone or partly from thorns and partly from sticks, all gradations between the two types being found.

Apart from Mr. Fuller's paper noted above, I have found only one other publication wherein considerable attention has been paid to this species, viz. that by the Rev. H. A. Junod ('Bull. Soc. Neuchatel Sc. Nat.,' xxvii, 1898-99, p. 244), in which the following interesting and pioneer discussion is found:

"La plus grande de toutes, c'est l'*Eumeta cervina* (*Druce*) = *E. moddermanni* (*Heyl*). On la rencontre aussi aux bord du Zambèze et il est assez remarquable pour attirer l'attention.

"Le fourreau de la chenille se compose de petites branches réunies en un faisceau cylindrique au milieu duquel la larve se tient. Ces branchettes sont, la plupart du temps, coupées par les mandibules de l'animal à un rameau vivant de l'arbuste dit Nembé-Nembé (une sorte de Mimosa du genre *Cassia*). Mais on en rencontre aussi sur d'autres Mimosa à grandes épines blanches avec lesquelles les chenilles construisent leur maison. Le diamètre de cette construction pittoresque, que l'on voit se balancer aux branches, est de 2 à 2½ cm. quand la chenille à atteint toute sa grandeur. Auparavant, durant les premiers temps de son existence, la chenille s'entoure de brindilles d'écorce qu'elle remplace peu à peu par des bouts d'herbe, puis par des branchettes toujours plus grandes. Son évolution doit durer plusieurs

mois, sinon même des années. Elle peut demeurer des semaines sans manger (surtout à l'époque des mues). J'en ai rapporté avec moi plusieurs spécimens d'Afrique. Ils ont très bien supporté le voyage et ont recommencé à manger dans l'hémisphère nord comme si ce jeûne de trois à quatre semaines ne leur avait pas causé de malaise.

"C'est très curieux de voir ces chenilles, dont les premiers anneaux sont recouverts d'écailles blanchâtres, couper les poutres de leur demeure. J'en ai surpris une qui avait déjà mordu une branchette de l'arbuste dit 'Djopfa' et l'avait fixée sur son fourreau au moyen de la soie qu'elle secrète. Elle voulut couper un second bout du même rameau, mais il était parvenu à cet endroit là d'une branchette latérale portant des feuilles très développées. Lorsque, avec ses mandibules, la chenille avait opéré la section, le bout de rameau tomba, car il était trop lourd. Elle ne se découragea pas pour si peu et je la retrouvai en train de couper un troisième bout. Elles réussissent à merveille à mesurer ces branchettes qui sont toutes de même longueur. Cependant, un ou deux d'entre elles dépassent en général les autres par en bas. C'est, je crois, pour fournir un appui à la femelle aptère lorsque elle est éclosée et qu'elle laisse son corps sortir un peu à l'orifice inférieure du fourreau en vue de l'accouplement.

"Le male éclôt à l'heure du midi. Dès le coucher du soleil il se met à voler en quête de femelles. J'en ai attiré jusqu'à une vingtaine à la fois, à toutes les saisons de l'année, lorsque j'avais une femelle récemment éclosée. Lorsqu'il a découvert celle-ci, après avoir volé en cercles concentriques autour de son fourreau durant quelques instants, il se fixe contre les poutrelles qui proéminent, introduit son abdomen dans le fourreau et réussit à l'allonger énormément pour aller féconder la femelle dont la tête sort à l'extérieur, mais dont l'oviducte se trouve au fond du cylindre. Elle dépose alors les œufs dont elle était pleine dans la chrysalide (il y en a plusieurs milliers), elle les enveloppe d'un duvet soyeux brun dont elle est recouverte. Après cette opération elle est diminuée des deux tiers et ne tarde pas à périr. Les petites chenilles s'éclosent bientôt (douze jours plus tard) et se répandent au loin à la manière des araignées en filant de longs bouts de soie au moyen desquelles elles s'accrochent là où le vent les mène."

Systematic Position.—The species belongs to the family Psychidæ, subfamily Eceticinæ, and was described by Heylaerts under the name of *Eumeta moddermanni*, while Janse places it in Walker's genus *Clania*. The species has been described from male specimens only; the female has not been described.

THE EGG.

Egg 0.90 by 0.60 mm., creamy white; egg membrane colourless, smooth, without sculpture. No micropyle could be observed. The eggs are packed closely together in the chrysalis shell of the female and mixed with hairs from its abdomen.

When the time of hatching draws near, the eggs change in colour to a dirty grey, the entire larva being plainly visible.

Number.—The eggs laid by a female are very numerous, ranging from 2–4000 and over. Eggs counted from four different females gave the following numbers: 2293, 3047, 3307, and 4433, the fecundity being thus apparently still greater than in the case of *Acanthopsyche junodi*.

Deposition.—The eggs are laid in the chrysalis case in a compact mass, mixed with the hairs and scales from the body, the case remaining inside the bag. When the full quota has been laid, we find the chrysalis case filled for two-thirds of its length, while the spent and shrivelled female either remains at the neck of the bag or drops to the ground. The young hatch in this protected situation and emerge on the first favourable day.

Incubation Period.—This was found to be fifty-four days in one case where the date of copulation with a virgin female was actually observed—i. e. from September 24th till November 19th—and this period thus corresponds closely with that of the Wattle Bagworm.

The Rev. Junod states that the young appear twelve days after copulation, but it is quite possible that he based his statement on field observations. As the period of flight of the males extends over nearly two months (the earliest moth observed by us was seen on August 25th, and the last October 21st), it is quite probable that the time between the last flying males and the first young larvæ noticed should be some twelve days only; or, if based on actual observation, it may be that the female had been fertilised some time previously, and was visited by another, late flying, male. Our female was reared

from a larva in the laboratory, was virginal, and visited only once by the male, then removed and kept under observation until the young appeared.

LARVA, FIRST INSTAR.

Length 1.5 to 1.9 mm. Ground colour cream (XVI), head black, dorsal thoracic shield and suranal plate vandyke brown (XXXIII). Thoracic legs bone brown (XL), dorsal plates on the 8th abdominal segment and leg-plates of anal prolegs verona brown (XXIX), setiferous plates on abdominal segments drab (XLVI).

The larva is slightly compressed dorso-ventrally; thoracic segments massive, abdomen held elevated, with last two segments deflected ventrally. Third thoracic segment the largest, from where the abdomen gradually tapers posteriorly.

Head.—Width of head-case 0.43 mm., adfrontals not separated from the parietals. Frons large and massive, nearly equilateral. Clypeus not separated from the frons.

Position of Setæ: (a) Postero-dorsal Region.—Setæ and punctures are congregated on the lower third, the upper two-thirds carrying several secondary tubercles or punctures (text-fig. 11, B). Pd. 1 at about the same height as adfr. 1; puncture pd. 1*a* closely approximated to pd. 1 and medial; pd. 2 medio-dorsal to pd. 1 below adfr. 2; puncture pd. 2*a* latero-dorsal to pd. 2 and placed far lateral, about dorsal to ad. 2.

(b) Antero-dorsal Region.—Ad. 1 at about the same height as puncture f.*a*, medio-dorsal to the first ocellus; ad. 2 and ad. 3 high, closely approximated; ad. 3 about level with pd. 1; ad. 2 about midway between ad. 3 and pd. 1, slightly below a line connecting these two. Puncture ad. 2*a* apparently absent.

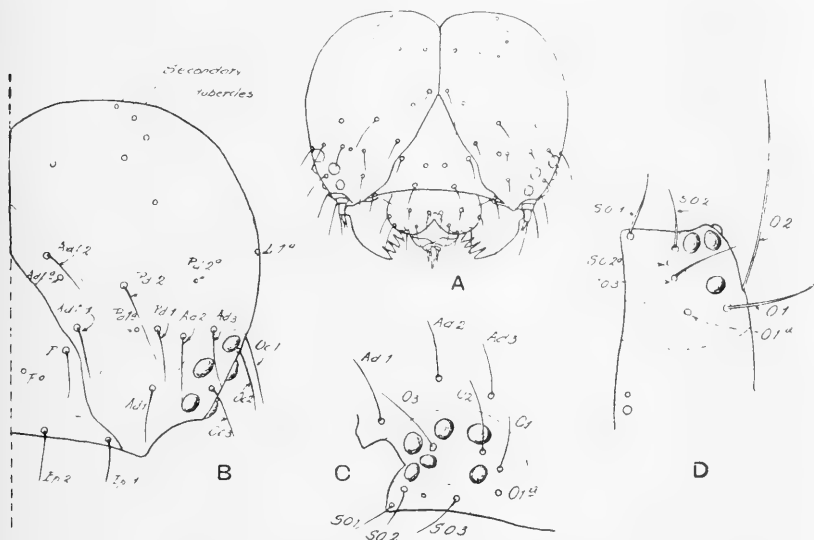
(c) Lateral Region.—Only puncture l. 1*a* could be seen, no seta l. 1. Puncture at about the same height as adfr. 2.

(d) Adfrontal Region.—Adfr. 1 close to and above f.; adfr. 2 near top of frontal. Puncture adfr. *a* close to adfr. 2.

(e) Frontal Region.—Frontal punctures closely approximated at about one-third of the height of the frons. Frontal setæ latero-dorsal to frontal punctures.

(f) Clypeal Region (Epipharyngeal Region).—Ep. 1 close to lateral corner, distance between the two ep. 2 about equal to that between ep. 1 and ep. 2.

TEXT-FIG. 11.



Clania moddermanni (Heylaerts). Larva, first instar.

A. Front view of head, showing position of setæ. $\times 80$. B. Left side of head with regions indicated and showing position of setæ. $\times 150$. C. Latero-ventral view of ocellar area with regions indicated and showing position of setæ. $\times 150$. D. Ventral view of sub-ocular area, showing position of setæ. $\times 300$.

(g) Sub-ocular Region.—The normal three setæ and one puncture are present (text-fig. 11, c, d). S.o. 1 marginal at medio-cephalic corner; s.o. 2 near anterior margin; s.o. 3 directly behind s.o. 2, near the latero-caudal corner of the region. Puncture s.o. 2a almost half-way between s.o. 3 and s.o. 2 and a little medial to a line connecting these two.

(h) Ocellar Region.—Seta o. 1 placed latero-caudal to the hind ocellus. Puncture o. 1a medial to seta o. 1. Seta

o. 2 between the two posterior ocelli; seta o. 1 at about the centre of the triangle formed by the o. 1, 5, and 6. O. 5 crowded out behind o. 1 and 6.

(i) Gular Region.—Gular puncture g. 1a and seta g. 1 situated straight behind o. 1a.

Mandibles.—Mandibles rather large, projecting far beyond the labrum, subquadrate, 5-toothed, the three first teeth sharp, the second one the longest (without step, as in *A. junodi*); the inner two small and blunt. Mandibular setae md. 1 and 2 close together at end of lower fourth of mandible (text-fig. 12, f).

Antennæ.—Short and thick, second joint about as broad as long, third and fourth together shorter than the second. No seta 1 on second joint could be found (text-fig. 12, i).

Maxillæ.—Maxillary lobes unequal; the median longer than the lateral and curved laterally. First joint of palpus with conspicuous sense-organ at base. Cardo large and long, extending beyond the submentals (text-fig. 12, d).

Labium.—With large acute triangular mentum. Submentum narrow, with cephalic angle very acute and caudal margin short (text-fig. 12, c).

Thorax and Abdominal Segments.—The arrangement of the body setae corresponds with that described for the first instar larva of *Acanthopsyche junodi*. Abdominal and anal prolegs with sharply pointed hooklets, of half the

Segment.	1.		2.	
	Right.	Left.	Right.	Left.
Abd. 3 .	11	10	12	12
Abd. 4 .	13	12	13	13
Abd. 5 .	13	12	11	13
Abd. 6 .	10	10	11	11
Anal .	8	9	10	12

number present in the late instars (text-fig. 12, E). The numbers are not constant, as shown in the table on p. 178, resulting from the examination of two specimens.

The number varies from 10 to 13 for the abdominal and from 8 to 12 for the anal prolegs.

The subsequent instars up to the penultimate are not known.

PENULTIMATE INSTAR (FEMALE).

Length of larva 37 to 40 mm. Ground colour pinkish buff (XXIX), changing to avellaneous (XL) on the abdominal segments. Markings on head and thoracic shields black; dorsal aspect of abdominal segments 3 to 10 fuscous black (XLVI). Spiracles orange cinnamon (XXIX), median area of under side of abdominal segments and setiferous plates on side bister (XXIX). Thoracic legs and hooks of prolegs fuscous black (XLVI).

Head.—Width of head-case 4 mm. Parietal cleft deeper than in the first instar.

Postero-dorsal Region.—Upper part of head greatly enlarged as compared with the first instar, as a result of which the postero-dorsal setæ are now placed nearer to the lower part of that region. Punctures pd. 2a and pd. 1a could not be seen (text-fig. 12, A).

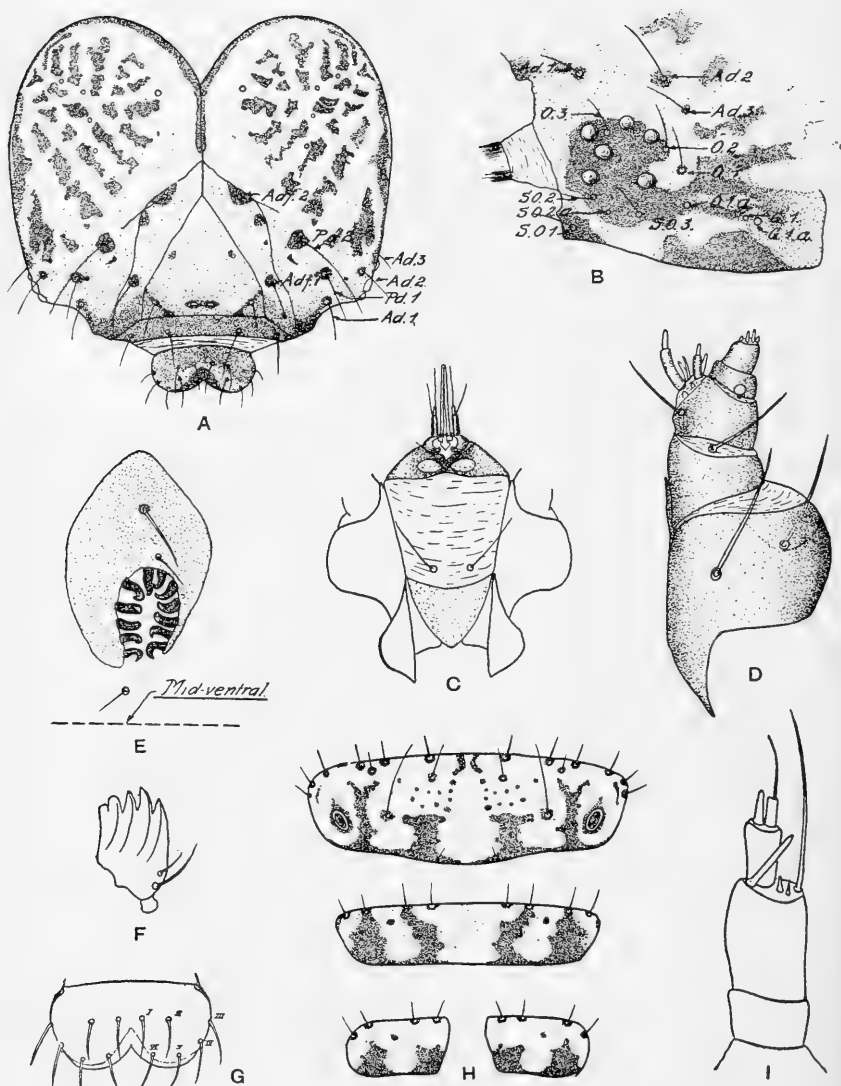
Antero-dorsal Region.—Relative position of setæ the same as in the first instar.

Frontal Region.—Frons relatively shorter than in the first instar, frontal punctures near median line, placed at lower one-fifth of the height of the frons. Frontal setæ only slightly higher than the punctures.

Adfrontal Region.—Adfrontals distinctly separated from the parietals, broad and massive; relative position of setæ the same as in the first instar.

Clypeal Region.—Clypeus distinct from the frons. Setæ 1 and 2 closer together than the 1 of each side.

Ocellar, Sub-ocellar and Gular Region.—Ocellus 6 placed between and behind a line connecting ocellus



Clania moddermanni (Heylaerts). Larva.

- A. Front view of head of full-grown larva. $\times 15$. B. Latero-ventral view of ocellar area, showing pattern and position of setae. $\times 30$. C. Labium, first instar. $\times 50$. D. Maxilla, first instar. $\times 100$. E. Abdominal leg with hooks, first instar. $\times 50$. F. Mandible, first instar. $\times 50$. G. Labrum, first instar. $\times 50$. H. Dorsal thoracic plates, showing pattern, full-grown larva. $\times 8.5$. I. Antenna, first instar. $\times 150$.

1 and 5. Relative positions of setæ the same as in the first instar (text-fig. 12, B).

The distinctive pattern on the head is shown in text-fig. 12, A. It does not lend itself readily to description.

Thorax.—Pattern of dorsal thoracic plates as shown in text-fig. 12, H. Relative positions of setæ correspond to those described for *A. junodi*. Prothoracic spiracle piercing the dorsal shield.

Abdominal Segments.—Transversely wrinkled on dorsal aspect. Segment 3 with one, posterior 4 and 5 with two, and 6 with one, anterior, transverse pustular bands. The arrangement of the setæ and setiferous plates similar to that of *A. junodi*. Anal plate uniformly coloured. Hooks of prolegs numerous, arranged in a single loop, opened medio-caudally. The number of abdominal hooklets is not constant, as shown in the following table :

Segment.	1.		2.	
	Right.	Left.	Right.	Left.
Abd. 3 .	23	24	22	22
Abd. 4 .	22	21	21	24
Abd. 5 .	20	20	22	21
Abd. 6 .	18	23	22	20
Anal .	20	21	21	23

Those on the anal legs in the two specimens examined range from 20 to 23; those on the abdominal legs from 18 to 24.

ULTIMATE INSTAR (MALE).

Length 22 to 25 mm. Colour pale; ground colour pinkish buff (XXIX), markings on head and thoracic shields only faintly indicated in sayal brown (XXIX) and bister (XXIX);

dorsal aspect of abdominal segments 3 to 7 clove-brown (XL). Anal plate of ground colour spotted with bister (XXIX).

Width of head-case 3 mm. Mandibles reduced in size. Number of hooklets on prolegs and the setal arrangement do not change as compared with the previous instar.

HABITS OF THE LARVA.

The first act of the young larvæ after emergence is to construct a small conical bag. This is a silken case, covered with minute particles of the parent bag. This behaviour is different from that of the larvæ of *A. junodi*, which do not construct their bag until distribution has taken place, the bag being formed from particles of the leaf on which they have been feeding. In *C. moddermanni* the larvæ are apparently distributed after the first bag is made. These young bagworms, when placed on a wattle tree, did not feed, but began to spin threads, by which they let themselves down and were blown by the wind. We did not observe a pronounced phototropism. At first the bag remains conical, then it becomes more cylindrical, but only after it has reached a length of about 15 mm. does the caterpillar begin to add the characteristic parallel sticks to its covering. These are at first cut from the mid-ribs and pedicels of the leaves; later on pieces of the twigs are bitten off. The twigs are fitted closely side by side and are attached over the entire length of the bag (Pl. XIII, figs. 9-13). We have not been able to observe clearly the method by means of which this attachment takes place. With one larva in the laboratory we noted that the twig was severed and thrown back and attached at first only at the mouth (upper end) of the bag, while the larva kept on feeding. Later in the day, towards evening, we found that the inner bag had been split lengthwise at the place where the new stick was situated, and the next morning we found the new addition firmly in place between the older parts of the bag. It thus appears that the additions to the bag are made at night, and the attachment is probably done from the inside. To attach a stick from the outside over its

entire length would make it necessary for the larva to leave its bag—a procedure which would be highly dangerous, and almost impossible. The older and smaller twigs are probably removed as the larva grows and are replaced by larger ones, as it is noticed that the mature bags contain none of the small, thin sticks which form the bags of the younger larvæ.

The sticks are approximately of equal length, but in the bags of the mature larvæ we find usually one or two of the sticks longer than the others and projecting beyond the lower end of the bag. Fuller claimed that these longer sticks were probably for the male moth to alight on, to facilitate copulation, while the Rev. Junod supposes that they would be a protection for the female when she exposes the anterior part of her body, preventing her from falling out. Neither of these explanations appear to be correct. If Fuller were right in his supposition, then these projecting sticks would be found mostly or exclusively on the female bags; but we found that the male bags invariably present these longer sticks, while on the female bags they are very often absent. Also, the twigs are too far away from the centre of the bag to allow a male, alighting on them, to insert its abdomen through the neck of the bag for copulation. Against the Rev. Junod's proposition we must mention that those sticks which may be present on the female bags are also too far away from the centre to be of any assistance to the female. As a matter of fact we found a great many females dropping out of their bags when the males were tardy in their appearance or were prevented from getting access to the females.

We have observed that these projecting sticks are made use of in the emergence of the male moth. The male pupa works itself more than half-way out of the bag, and the moth, emerging, endeavours to grasp one of them with its legs, and is thereby given a purchase to withdraw its abdomen from the pupa-case. It then rests on the twig while its wings are expanding and hardening.

The larvæ of *C. moddermanni* do not show the gregarious instinct which is found so highly developed in *A. junodi* towards the end of the larval period, nor do they conceal themselves by moving towards the centre of the tree at the time of pupation. The bags hang singly and fully exposed, the strong compact case being probably sufficient protection against any interference from an outside enemy.

Food-plants.—Of these, *C. moddermanni* has a great variety. At Ladysmith, Natal, during a period of heavy infestation, the writer found this species living on the following trees and shrubs: peach, apricot, plum, quince, apple, pear, loquat, cherry, pomegranate, oak, privet, roses, *Macrocarpa*, black wattle, various species of thorn tree (*Acacia*), and an occasional specimen on citrus trees, while from Pretoria specimens were obtained which had subsisted entirely on the pepper tree (*Schinus molle*), and at Winkelspruit, Natal, a few specimens were found on an *Eucalyptus*. The individuals from the pepper tree were on the average very much smaller than normally, and were much behind in their development, so this plant appears to be less favourable to them. It has not been found on the silver oak (*Grevillea robusta*), nor on the wild syringa (*Melea azedarach*), and since these were standing amongst heavily infested trees at Ladysmith they appear to be immune.

The Bag.—Cylindrical, consisting of an inner layer of white silk covered with short twigs or thorns of the food-plant. These twigs are subequal in length, placed parallel and contiguous, and are attached over the entire length of the bag, forming a compact, strong case. Usually, especially in the case of the male bags, one or two, or even three of the sticks are much larger than the others, and project below the neck of the bag. If there are two these are usually placed about diametrically opposite each other. The upper and lower ends of the bag are free and movable, the silken lining being covered only with minute fragments of bark or dry leaves (Pl. XIII, figs. 9–13).

Length of male bags 25 to 35 mm., female bags 30 to 55 mm.

THE PUPA.

Pupation.—The caterpillars do not stop feeding until some time in May or June if there be still food. After this feeding period and before pupation the caterpillar undergoes a moult, which is different from the others in that during the time between this moult and pupation no feeding takes place, and the larva remains pale-coloured, the same as was observed in the case of the Wattle Bagworm. This stage is short, probably only a week or two (no actual data are available), after which pupation takes place. Here no inner bag or cocoon is made such as we saw in the Wattle Bagworm, the cavity between the pupa and the case being merely filled up with soft, fluffy white silk, while an extra layer is added to the inside of the covering. The bag is not fastened by means of a band around the twig or stem, but it is merely broadly attached to its under side, so that no damage to the food-plant is caused, such as the girdling we saw resulting from the attachment of the Wattle Bagworm.

Pupation takes place during June and July, the length of the pupa stage being probably about two months, as the moths have been noticed from August 25th until the end of September.

Male Pupa.—Length of pupa 15 mm., width 4 mm. at place of greatest width across insertion of front wings. General form slender, thoracic part only slightly wider and deeper than the abdomen; the last three segments of the abdomen slightly curved ventrally. Posterior edges of abdominal segments 4 to 7 prominent, wider than their anterior edges, giving the pupa a telescoped appearance. General impression of sculpture smooth, sub-shining, with the dorsal part of the prothorax rugose. Colour dark reddish-brown; prothorax, dorsal aspect of abdominal segments 1 to 4 and antennal cases darker than the remainder of the pupa, while the head is distinctly lighter in colour.

Head somewhat deflexed ventrally, and rather definitely set off from the body. Vertex with median carina (cocoon breaker). Clypeus quadrate; paraclypeal pieces elongated, flat, rugose, directed laterally. Labium pointed, labial palpi not visible. Maxillary palpi broad, triangular, without a distinct lateral lobe. The region across maxillary palpi and labium transversely impressed. Head sub-shiny, finely transversely striatulate on vertex, eye-spot glabrous. Antennal cases broad at basal half, attenuated distally, rather short, reaching caudally not as far as the first leg-cases (text-fig. 13, A, C, E).

Prothorax with a continuation of the cephalic median carina, strongly longitudinally sulcate, and with a transverse sinuate ridge. Mesothorax large, shining, with a median raised area. There is a prominent setiferous small tubercle on each side of the median line at about two-thirds its width from the anterior edge. Two pairs of smaller similar punctures are found, one lateral, and one latero-anterior to the setiferous tubercle mentioned. Front wing-cases reach ventrally to nearly the posterior edge of the 3rd abdominal segment. Metathorax very narrow in median line. Lateral angle of posterior wing-cases very obtusely rounded; these wing-cases disappear behind the primaries at the middle of the 3rd abdominal segment. There is a small setiferous puncture on each side of the median line near the anterior edge of the metathorax.

Abdominal segments transversely striated on dorsal aspect, segments 1 to 5 very dark, the following segments lighter in colour. Posterior margins broad, smooth, and light-coloured. Posterior edge of abd. 2 and 5 with a dorsal row of minute,

TEXT-FIG. 13.—*Clania moddermanni* (Heylaerts).

- A. Dorsal view of anterior part of male pupa. $\times 7$. B. Dorsal view of posterior part of male pupa. $\times 7$. C. Ventral view of anterior part of male pupa. $\times 7$. D. Ventral view of posterior part of male pupa. $\times 7$. E. Side view of male pupa. $\times 3.3$. F. Dorsal view of female pupa. $\times 3.3$. G. Ventral view of female pupa. $\times 3.3$. H. Ventral view of anterior part of female pupa. $\times 15$. I. Side view of female. $\times 3$.

6



recurved teeth pointing anteriorly. In addition to this, all segments 2 to 9 have near the anterior edge a row of strongly chitinated spines directed caudally and arranged in a crescent-shaped line. These spines are only slightly developed on abd. 2 to 5 and 9, but are conspicuous on abd. 6, 7 and 8, reaching their greatest development on the last segment.

On the ventral aspect abd. 4 to 6 show the scars of the larval prolegs, and in addition, abd. 3 to 7 have a lateral semilunar chitinous plate. Abd. 9 shows strongly developed genital tubercles, while on segment 10 the cremaster is absent, but the anal prolegs have developed into two divergent, flattened, conical plates, compressed laterally, and each ending in a strongly curved hook directed ventro-anteriorly (text-fig. 13, B, D).

The abdominal segments show setae, corresponding in position to the primary setae of the caterpillar.

Female Pupa.—Length 20 to 23 mm., width 6 mm., sub-cylindriform, with caudal end rather abruptly pointed, anterior end rounded. Colour mahogany red (II) to hessian brown (XIII).

Pupa vermiform, without wing-cases, eyes, antennae or distinct mouth-parts. Ventral aspect of head so greatly wrinkled as to obscure the parts of which it is composed (text-fig. 13, H). Head deflexed and retracted under prothorax. Legs rudimentary, showing as short, compact, flattened, paired, free appendages on a broad base, arising from the ventral aspect of the three thoracic segments. Prothoracic spiracle obscure, other spiracles prominent. Ventral aspect of abdominal segments smooth, scars of abdominal and anal prolegs conspicuous. Dorsal aspect of thoracic and abdominal segments transversely striate. Abd. 1 with a row of minute hooks on the edge of the caudal declivity; segments 2, 3 and 4 have two similar rows of hooklets, one at the cephalic and one at the caudal end, while abd. 5, 6, 7 and 8 each have only one sinuate row of hooklets near the cephalic edge, increasing in size and prominence toward the 8th segment, on which they reach their greatest development. On

abd. 9 this row is represented by four short conical spines, while the 10th segment bears a cremaster, consisting of two small hooks, directed ventro-caudally, placed on a rather broad, oval base (text-fig. 13, F, G).

THE IMAGO.

Emergence.—The males emerge usually about midday, or some time during the afternoon. The pupa works down through the neck of the bag until it projects free for over half its length. Being slightly curved ventrally, the head of the pupa extends horizontally to a considerable extent, and the moth, upon breaking the pupa-case, is able to reach one of the long twigs, which it grasps with its legs and pulls the remainder of its body out of the case. It then remains quiet on the twig to allow its wings to expand and dry. The entire process of emergence from the moment the pupa-case splits until the moth is ready to fly takes about fifteen to twenty minutes, and immediately after this it flies forth in search of a female.

The vermiform female does not emerge in the true sense; only the top of the chrysalis is pushed off. The first indication of the female being ready to receive the male is the appearance of a quantity of the brownish fluffy silk protruding from the neck of the bag, having been pushed out by the descending female. If the male be tardy in making its appearance the female protrudes its head, then its thorax, progressing further and further until it loses all purchase and drops out of the bag and dies on the ground.

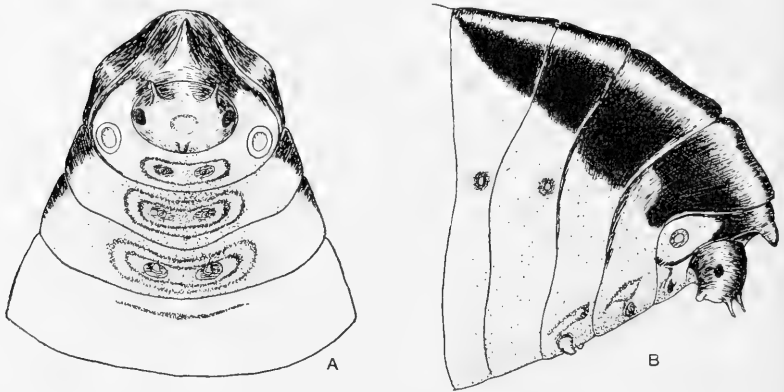
Female.—Length 20 mm., width 6 mm., vermiform; body-wall membranous with the exception of the head and dorsal part of the three thoracic and first two abdominal segments (text-fig. 13, I).

General colour light pinkish cinnamon (XXIX), chitinated parts of head, etc., ochraceous orange (XV), ventral aspect of thorax and two first abdominal segments deep vinaceous grey (L), hairs around 7th abdominal segment cinnamon buff (XXIX) tipped with sayal brown (XXIX).

Head conical, deflexed ventrally, with small, black, lateral spot (eye-spot) and two sharp, laterally diverging prongs, directed ventrally. Mouth-opening transversely oval, buccal region membranous. Head concealed under prothorax (text-fig. 14, A, B).

Prothorax also facing ventrally. Sternal part narrowed. Pronotum with a short, curved, median prong, directed ventrally. Dorsal part only chitinised, spiracular and ventral

TEXT-FIG. 14.



Clania moddermanni (Heylaerts). Female.

A. Ventral view of anterior part of female. $\times 20$. B. Side view of anterior part of female. $\times 20$.

region membranous. Prothoracic legs rudimentary, showing only as a pair of small chitinous plates, each with a minute hooklet. Mesothorax, metathorax and 1st abdominal segment with a median dorsal ridge. The chitinised area extends from the dorsum over the lateral aspect to about opposite the prothoracic spiracle on the mesothorax and decreases in size on the succeeding segments to the 2nd abdominal. Other abdominal segments membranous, transparent, showing the ovarian tubes filled with eggs.

Thoracic legs of meso- and metathorax also rudimentary, those on the metathorax slightly less so than on the pro- and mesothorax.

Abdominal segment 7 adorned with a fringe of hairs and hair-like scales near its posterior edge. Eighth abd. segment much smaller than the preceding ones, annular, bearing the genital opening ventrally on a small membranous cone directed forwards. No genital armature. Ovipositor blunt, conical, directed ventro-posteriorly, strengthened on its dorso-lateral aspect by two chitinised rods.

Copulation.—Copulation takes place in a manner similar to that described under the Wattle Bagworm. In one case observed in the laboratory copulation started at 2.37 p.m., and lasted until late in the afternoon (after 4 p.m.). The exact length of time was not noticed, but by 6 p.m. the sexes had separated. In the open I have seen the males flying in the late afternoon (5.30 p.m.), while the Rev. Junod states that the male flight occurs after sundown.

Dispersal.—The dispersal takes place during the first instar of the caterpillar and is mainly caused by the wind and air-currents, in a manner similar to that described under the Wattle Bagworm. Notwithstanding the great fecundity of the female (averaging some 3300 eggs), the species is not as common nor as widely distributed as the Wattle Bagworm. The mortality amongst the young must be very great, and it is probable that in this species the young, as yet, do not so readily adapt themselves to a variety of food-plants, and they do not thrive so well on the wattle.

Geographical Distribution.—This species appears to be widely spread all over South Africa, but seems to thrive best on the high veld. A few isolated specimens have been found at Winkle Spruit, Natal Coast, but it appeared much more abundant at Ladysmith, Natal, and Pretoria, Transvaal, while specimens have been collected at Christiania, Louis Trichardt, Hill Crest, and Mid-Illovo. It has also been mentioned by the Rev. Junod as occurring in Portuguese East Africa.

Economic Importance.—For the present, outside of the native thorn trees, the species shows a predilection for various fruit trees, mostly of the pomaceous group, and for oaks. On the former it may in some seasons cause great damage. In

Ladysmith the infestation was especially heavy during the season of 1915, the orchards in that town suffering severely. An idea of its abundance can be gained from the fact that a certain Mr. Sharp, during the winter cleaning of his orchard, destroyed over 20,000 bags on a plot of three-quarters of an acre.

In the course of time there is little doubt that this bagworm will become adapted to the black wattle, and it will then be a far greater plague than the Wattle Bagworm, *A. junodi*.

Parasites and Diseases.—Fortunately the Lictor Bagworm is very heavily parasitised. A lot of sixty-four bags, collected in Pretoria, contained only ten apparently healthy larvæ, more than forty having been attacked by dipterous parasites of the family Tachinidæ. Furthermore, a species of *Pimpla*, probably identical with that parasitising the Wattle Bagworm, also attacks the Lictor, while two smaller hymenopterous parasites have been reared in abundance from this bagworm. It is also subject to a fungus disease which at times destroys a great number.

These natural agencies are at present very effective in keeping the species under control, and seasons of great abundance are followed by years when it is hardly noticed. In this respect the Lictor Bagworm is now in the same stage as the Wattle Bagworm some ten years ago.

5. *Manatha æthiops* *Hampson*. Pl. XIII, fig. 15.

Manatha æthiops *Hmpsn.* A.M.N.H. 1910 (8), vol. vi, p. 116.

Psyche (*Manatha*) *æthiops* (*Hmpsn.*) Janse, Ann. Natal Mus., 1917, vol. iii, pt. 3, p. 600.

This species was once bred by the writer from a number of bags found on a silver wattle (*Acacia dealbata*) at the Westfalia Estates near Tzaheen, Zoutpansberg District, Transvaal. The bags were clustered together for pupation, attached to the sides and under surface of a branch by short stalks. Unfortunately no larvæ or pupæ were preserved at the time, and, as I have not had an opportunity to collect this species again, the immature stages remain for the present unknown. The specimens were collected in March, 1910; the adults emerged on April 20th.

The type has been described by Hampson from Cape Colony, and so the species seems to have a fairly wide distribution throughout South Africa.

The bag of the full-grown larva is 25 mm. long by 3 mm. wide, suspended from the branch by a cord 5 mm. long. The bag is nearly cylindrical in shape, slightly narrower at the bottom; its upper end is drawn out into a pointed cone about 3 mm. long, and its lower end is cut off square (Pl. XIII, fig. 15). The bag is composed of tough, grey silk, covered with small particles of some material, the origin of which could not be ascertained. Where the bag is attached to the twig, the suspending cord of closely woven silk strands is expanded into a round, flat plate, about 4 mm. in diameter (text-fig. 15, c).

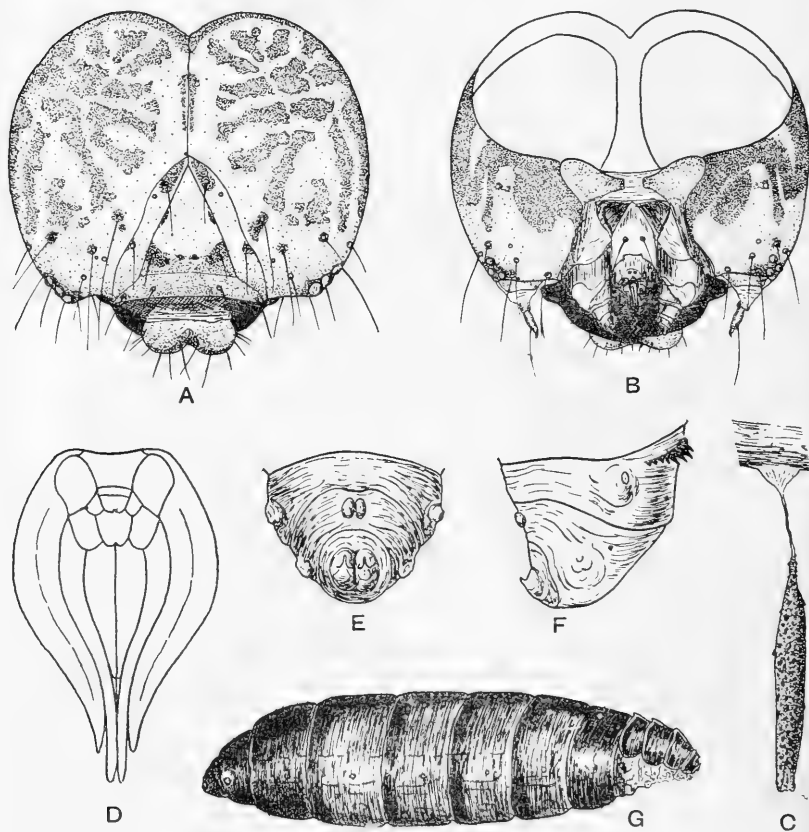
The moth is of a different type from that of the genus *Clania* or *Acanthopsyche*, being broad-winged and uniformly dark in colour. The body is rather weak, and from the general appearance of the moth we may conclude that it is not a strong flier. "The wings are thinly covered with buffy brown (XL) hairs" (Janse).

Male Pupa.—Described from a broken pupa-case from which the male had emerged. Length 8 mm. The width could not be determined, as the pupa was broken. Wing-cases reach to the anterior third of the 3rd abdominal segment. Front of head truncated, eyes large, paraclypeals distinct, rugose. Maxillæ short, maxillary palpi large, prominent, finely rugose. Antennal cases wide, longitudinally deeply and widely sulcate, faintly striate transversely. Abd. segments 3 to 7 smooth, shining on ventral surface on anterior half, punctulate and matte on posterior half. Dorsal aspect of abdominal segments transversely striate; segments 1 to 3 unarmed, 4 with a small posterior, 5 to 8 with an anterior row of spines, shortest but most strongly developed on the 8th segment. Cremaster feeble, consisting of two small hooks on broad, elliptical bases, directed ventro-anteriorly (text-fig. 15, d, f).

Female Pupa.—Described from an empty pupa case found in bag. Length 10 mm.; cylindrical, anterior dorsal

surface curved downwards from 1st abdominal segment to head, posterior part from caudal edge of 8th segment abruptly

TEXT-FIG. 15.



Manatha æthiops Hamp.

- A. Front view of head of full-grown larva. $\times 27$. B. Ventral view of head of full-grown larva. $\times 27$. C. Bag of full-grown male larva, showing method of attachment. $\times 1\frac{1}{3}$. D. Ventral view of head and thorax of male pupa. $\times 7$. E. Ventral view of posterior part of male pupa. $\times 20$. F. Side view of terminal part of male pupa. $\times 20$. G. Side view of female pupa. $\times 7$.

rounded, conical. Pupa widest at the 8th abdominal segment (text-fig. 15, g). Head facing ventrally, concealed by

prothorax, small, membranous. Thoracic segments and 1st abdominal chitinised only on dorsal and part of lateral aspect, the remainder membranous. The rest of the pupa normally chitinised, segments 2 to 7 lightly so, except for a broad posterior band on each segment, which on the 2nd also extends over the entire ventral surface. Segments 8 and 9 more heavily chitinised, the 10th less than the preceding ones. No trace of a cremaster apparatus.

Surface of body finely granulate. Thorax and 1st abdominal segment with a dorsal ridge, increasing in height posteriorly on each segment, and at the hinder margin meeting a transverse ridge, which runs along the posterior edge of the segments. These segments are more coarsely rugose than the abdominal segments. Ventral surface of head and thorax much folded and wrinkled so that parts could not be made out. There seemed to be no trace of leg-cases.

The female moth upon emergence pushes the head part off, while the pro- and mesothorax split along the median dorsal line.

Abd. segments 2 to 7 finely transversely striated dorsally, especially the 2nd. Eighth segment with two lateral, conspicuous prominences on which the spiracles are situated.

6. *Manatha subhyalina* (Janse).

Psyche (*Manatha*) *subhyalina* Janse. Ann. Natal Mus., 1917, vol. iii, pt. 3, p. 601.

This species was described by Janse from three specimens (type and two co-types) captured at Umkomaas, Natal, January 4th to 24th, 1914. Through the courtesy of Mr. Janse I was supplied with a specimen of a bag, collected by Mr. Robinson at Grahamstown, and said to be that of this species. The bag contained a dead larva from which the accompanying drawings and descriptions have been made (text-fig. 16, d).

In February, 1918, the writer obtained a couple of bags, very similar in appearance to the one from Grahamstown, on a shrub (*Brachylæna discolor* D.C.) at the beach at Durban, one containing the remains of a female pupa, the



other a live male pupa (text-fig. 16, E, F). The pupæ are Psychid in character, and since the bags are similar and the locality is not far from that of the type, it is at present assumed that the pupæ are those of *subhyalina*.

The bag sent by Janse was 8 mm. long; the larva contained therein had died while in the act of moulting, so that it was not fully grown. The full-grown bags collected at Durban were 10 mm. (male) and 12 mm. (female) in length, and accordingly in size also these bags resembled the Grahams-town bag.

The Larva.—The caterpillar contained in the bag from Gramhamstown was dead and considerably shrunken, and therefore its normal length could not be determined. It is of the usual bagworm type, with radiating pattern on the head and large chitinised plates on the thoracic segments. The colour patterns, especially those on the thoracic segments, are not sharply defined as in the other Psychid larvæ, and here consist more of blurred pigmented areas, a condition also found on the vertex of the head, while the pattern on the remainder of the parietals is fairly clear and distinct (text-fig. 16, A, B, C).

The number of hooklets on the abdominal prolegs fluctuated in the specimens examined between 19 and 25; while the anal claspers were armed with 18 and 19 hooklets. The arrangement of these hooks was, as usual, in a single, transverse loop open at its medio-caudal aspect, but those on the caudal half of the loop appeared to be very much reduced and becoming rudimentary.

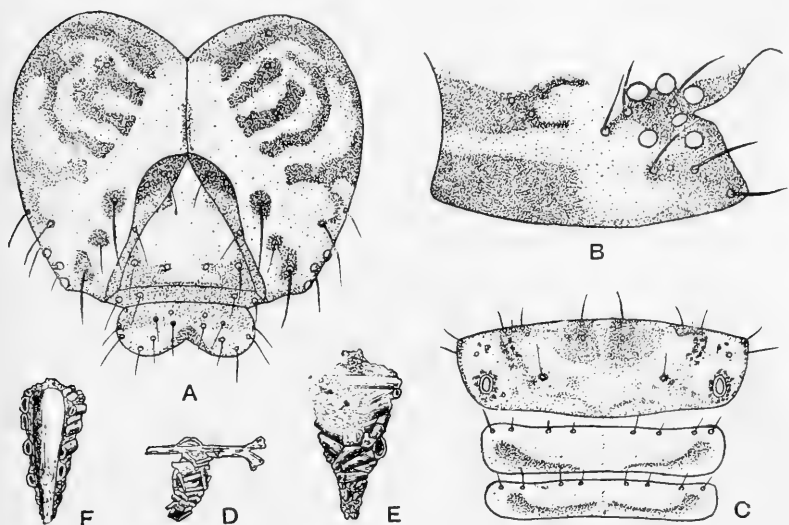
The bag of the mature larva is only about 10 mm. long in the male and about 12 mm. in the female; it is pyramidal and four-sided in shape, the sides being formed by rather neatly arranged transverse sticks, composed of the small twigs and midribs of the leaves of the food-plant. These are very much smaller at the lower end, rapidly increasing towards the mouth end. The sticks are rather thick as compared with the size of the bag. With approaching pupation the larva does not make an inner bag, but fills the cavity between

it and the wall with some loose white silk. This applies to both sexes. The pupæ are very large as compared with the bag, and they fill nearly the entire space.

When pupation approaches, the larva fastens the mouth of the bag very securely to the under surface of the leaf, and it takes considerable force to remove it.

The bags were found on the leaves of *Brachylæna*

TEXT-FIG. 16.



Manatha subhyalina Janse.

- A. Front view of head of full-grown larva. $\times 27$. B. Ocellar and sub-ocular area of head of full-grown larva, showing position of setæ. $\times 40$. C. Dorsal thoracic plates of full-grown larva, showing colour-pattern and setæ. $\times 13$. D. Bag of larva (from Grahamstown), showing attachment to mid-rib of leaf. $\times 1.3$. E. External view of bag of male pupa. $\times 2$. F. Opened bag of male pupa, showing smooth interior and absence of inner bag. $\times 2$.

discolor, a common shrub on the sand dunes at Durban, and were attached to the under side of the leaf. When collected the bags were mistaken for young specimens of *Gymnelema vinctus* Walker, but they can be distinguished from the latter by being four-sided, while those of *G. vinctus* are five-sided.

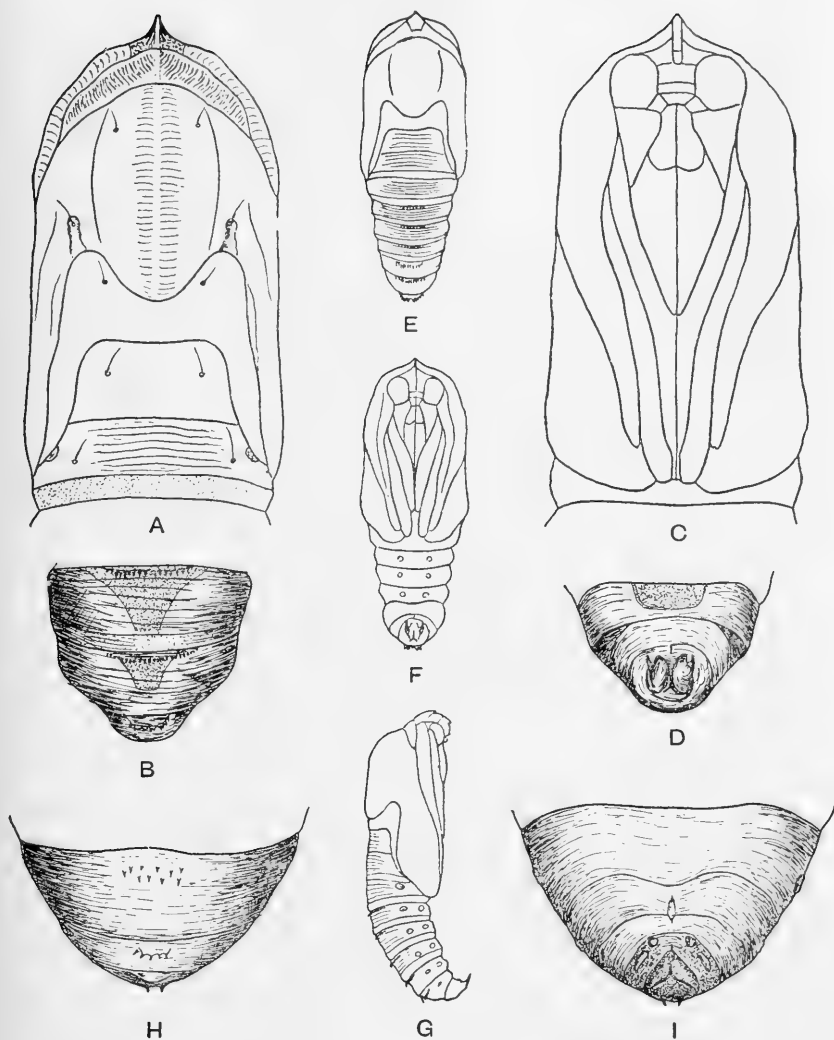
Pupa, Male.—Length 6 mm., width at shoulders 1·8 mm., depth 2 mm. Posterior part of pupa, including the last three abdominal segments, curved ventrally (text-fig. 17, A-G). Anterior end of pupa obliquely truncate from mesothorax to vertex. Head with a median carina with two small but sharp indentations, and with a small lateral ridge running from the top of the eye to the median carina. Head rugose. Area below the labium transversely sulcate. Maxillary palpi large, triangular. Clypeus and labrum short, transverse. Paraclypeals small, subquadrate. Antennæ broadened over the anterior two-thirds and not reaching the ends of the wing-cases, longitudinally sulcate, with numerous small transverse grooves. Wing-cases reach ventrally nearer to the posterior edge of the 3rd abdominal segment. Pronotum obliquely striate; mesonotum transversely striatulate. Metanotum and 1st abdominal segment strongly longitudinally striate. Abd. segments 2 to 7 transversely striate, 4 to 8 with an anterior row of small teeth, increasing in size towards the 8th segment. Abd. 9 unarmed; abd. 10 with two cremaster hooks on broad, conical bases, the hooks slightly diverging and curved cephalo-ventrally, and each with two additional protuberances at its cephalic end.

Anterior part of pupa (head and thorax) black, caudal portion of the wing cases natal brown (XL).

Pupa, Female.—From the remains of the female pupa which we had for examination it appears that it is distinctly Psychid in character. About 7 mm. long by 2·5 mm. wide, the widest part being at the 8th abdominal segment, from whence it tapers gradually anteriorly and abruptly posteriorly. Abdominal part of pupa smooth, glossy.

Abdominal segments finely transversely striated, with the intersegmental bands finely granulate. Abd. 7 with a small median, dorsal, toothed area, bearing some 10 small, pointed teeth, curved slightly posteriorly, arranged roughly in two transverse rows; the 8th segment with a similar, still smaller area with four rudimentary teeth; 9th segment with a low median dorsal knob, not armed; 9th and 10th segment finely

TEXT-FIG. 17.



Manatha subhyalina (Janse). Pupa.

- A. Dorsal view of anterior part of male pupa. $\times 20$. B. Dorsal view of posterior part of male pupa. $\times 20$. C. Ventral view of anterior part of male pupa. $\times 20$. D. Ventral view of posterior part of male pupa. $\times 20$. E, F, G. Dorsal, ventral, and side views of male pupa. $\times 7$. H. Dorsal view of caudal region of female pupa. $\times 13$. I. Ventral view of caudal region of female pupa. $\times 13$.

shagreened dorsally. Cremaster consists of two small slender hooks, rather widely spaced at the base, and this base set off dorsally from the remainder of the segment. On the ventral side we find the anal leg-scars large, triangular, flanked at their cephalic parts by two flattened, elliptical lobes, directed latero-anteriorly, and in front of these, two small, smooth, round papillæ (text-fig. 17, H, 1).

The thoracic segments carry a dorsal median carina and are transversely striated dorsally.

The Adult.—The male has been described by Janse as expanding 15 to 16 mm. with "head, thorax and abdomen above and underneath rather thinly covered with avellaneous (XLV) hairs, antennæ and the long branches blackish-brown (XLV), wings subhyaline, sparsely but regularly covered with avellaneous hairs on the upper and under side."

The female, judging from the remains of the pupa, is wingless, but we have not yet been able to obtain a specimen for description.

Of the habits of this species nothing is known. As the male has been captured at light the species is probably crepuscular or nocturnal in its habits.

The dates of capture of the males extend from January 4th to 24th, while the writer found a male pupa at the beginning of February. The imago had not emerged at the beginning of March, so that there is apparently a long flying season, and, presumably, only one brood a year.

The species is, for the present at least, not of economic importance. Parasites and predaceous enemies unknown.

7. Gibson's Bagworm (*Manatha* sp.) Pl. XIII,
fig. 16.

Fig. 16, Pl. XIII, shows a number of the bags of this species attached to a twig of Black Wattle (*Acacia mollissima* Wild.). All are fastened by means of a thick strand of silk usually about half as long as the bag. The exact locality of the specimens figured is unknown to me. Presumably they

were collected at Mahlabatini, Zululand, by Mr. J. Y. Gibson, the then Resident Magistrate. Mr. Fuller mentions this species in his Bulletin XIV of the Natal Department of Agriculture in 1909, and gave it the popular name of The Gibson's Bagworm after its discoverer.

From the photograph it appears that the gregarious instinct is developed in the later stages of the larval life, but not to the same extent as in the Wattle Bagworm (*Acanthopsyche junodi* Heyl.), where the bags actually touch each other. It is also possible that this clustering together is merely caused by the larvæ seeking similar favourable places for pupation.

Unfortunately no adults were bred from this material, and the identity of the species remains in doubt. But the bag is characteristically like those of other species of the genus *Manatha*—at least, such as are known to me—so that for the present we may feel safe in considering it to belong to this genus.

The bag of the full-grown larva measures 14 mm. in length by $2\frac{1}{2}$ mm. in diameter at its widest part near the top. It is circular in cross-section, slightly wider near the upper end. Here it abruptly narrows, and is attached to the twig by means of a strand of silk, from 6 to 12 mm. long. The bag tapers gradually towards the truncated lower end. The bag consists of thin, but closely woven, white silk, and is covered on the outside with minute grey particles. The nature of these could not be ascertained, but they may be minute pieces of the food-plant or, partly, excreta of the larva. At the lower fourth this covering is much thinner, and here the bag is closed by being put into several longitudinal folds. At the upper end the bag-covering continues for about half-way up the stalk, the stalk itself at the place of attachment to the twig being spread out into a roundish flat plate.

From the material examined it appeared that the female fills the bag with a thick mass of white silk, surrounding the pupa, although no true inner bag is made, such as we see in *Acanthopschye junodi*; in the male bags we did not find



this, but apparently the male is content with adding an extra layer of silk to the inside of the bag. Also, in the male bags (from which the moths had emerged), we find the last larval skin pushed out at the lower end of the bag; in the female this was found inside, pushed to the very top.

8. *Semimanatha fumosa* Janse.¹ Pl. XIII, fig. 17.

This species was found by the writer in December, 1916, on an oak (*Quercus pedunculata*) in Pietermaritzburg. The bags (text-fig. 19, I, K) bore a close resemblance to those of *Manatha æthiops*, and they were at first considered to be the half-grown stages of this species. However, the larvæ proved to be practically full-grown, and the moths, upon emerging, were sent to Mr. Janse for determination, and were described by him as a new species—*Semimanatha fumosa*, sub-fam. *Psychinæ*. The resemblance between the bag of this species and that of *Manatha æthiops* is very striking, and much greater than that between those of *M. æthiops* and *M. subhyalina*. A comparison of the larvæ of these two species would be very interesting. Unfortunately, up to the present no adequate larval material of these two species has been obtained which would allow of minute comparison, and the differences are as yet entirely based upon the characters of the adults.

Food-plants.—A careful search was made for the larva of *S. fumosa* on the wattle and native trees, but up to this time it has not been found, so that the normal food-plant is unknown. It has been found only on the oak (*Quercus pedunculata*) in the town of Pietermaritzburg, and, while the trees are plentiful, the bagworms could be found on only one or two stunted trees.

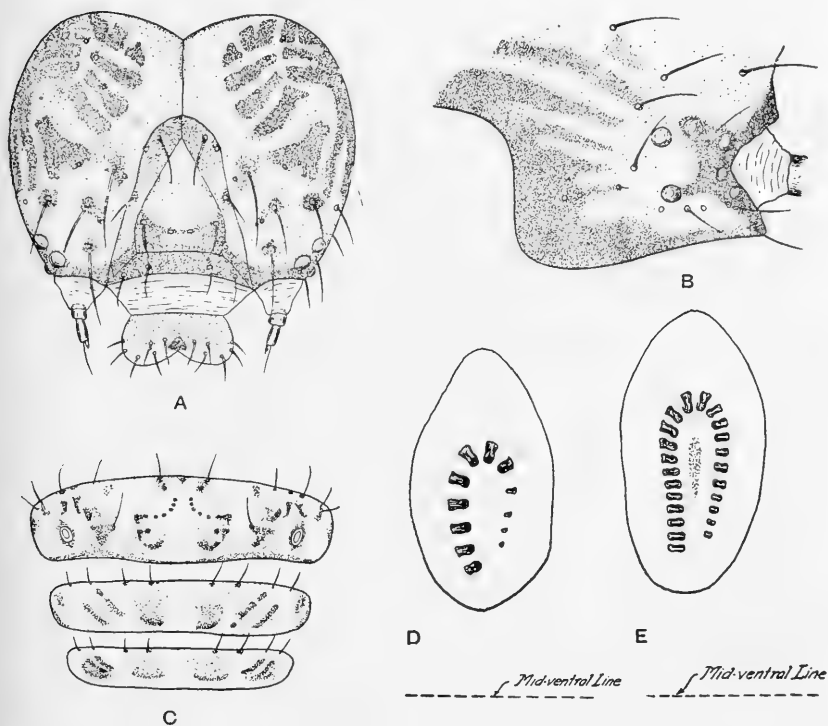
Larva, Full-grown.—Length of larva 10 mm., width of head-case 1.5 mm. Ground colour of head pale orange yellow (III), that of thoracic plates and anal plate pale yellow orange (III), of body-segments cartridge buff (XXX), setiferous plates on body-segments pale olive buff (XL).

¹ Described in Janse's paper preceding this, p. 139.

Markings on head ochreous orange (XV), on thoracic plates, anal plate, and on 8th and 9th abdominal segments argus brown (III).

Head partially retracted under the prothorax. Colour

TEXT-FIG. 18.



Semimanatha fumosa Janse. Full-grown larva.

- A. Front view of head, showing colour pattern and position of setae. $\times 23$. B. Ocellar and subocellar region showing setae. $\times 17$. C. Pattern on thoracic plates. $\times 23$. D. Arrangement of hooklets on proleg of 3rd abdominal segment, showing reduced number and rudimentary condition of posterior row. $\times 45$. E. Hooklets on proleg of 6th abdominal segment, showing normal number and development. $\times 45$.

pattern on the head radially arranged; setae all placed on the lower third of the epicranum (text-fig. 18, A, B). Colour pattern on the prothorax much reduced, as compared with

representatives of the genus *Acanthopsyche*, and diffused; that on meso- and metathorax indistinct (text-fig. 18, c). Body-segments with small setiferous plates bearing the primary setæ. The 8th abdominal segment with a small triangular dark area on each side of the median line; the 9th with the posterior half pigmented, while on the 10th the anal plate takes in nearly the entire surface of the segment.

The number of hooklets on the abdominal and anal prolegs are as follows:

Segment.	1.		2.		3.		4.	
	Left.	Right.	Left.	Right.	Left.	Right.	Left.	Right.
Abd. 3 .	13	10	14	16	12	10	14	14
Abd. 4 .	22	23	23	24	24	24	22	22
Abd. 5 .	22	22	23	24	24	22	22	22
Abd. 6 .	22	24	20	24	22	24	22	24
Anal . .	16	16	16	16	16	16	16	16

We thus see that in all the specimens examined the number of hooklets on the prolegs of the first leg-bearing segment is only approximately half the normal number. Besides, as shown in the figure, these hooklets are only very slightly developed, especially those of the posterior row (text-fig. 18, d, e). It is therefore clear that these proleg hooks are being reduced. On the other hand, the number of the hooklets on the anal legs is remarkably constant.

Habits of the Larva.—The behaviour of the newly-hatched larva and the formation of the bag have not been observed, while no data are at hand regarding the method of distribution. After the bags have been made and the caterpillars are feeding they show no tendency to congregate, but each leads a separate existence, feeding on the underside of the leaf. Those collected on the oak in Pietermaritzburg

showed little inclination to travel, and they attached themselves for pupation on the leaf on which they had been feeding.

The Bags.—When young, the bag appears as a narrow truncated cone, made up of minute particles of the food-plant attached to the inner lining. With approaching maturity the basal part of the bag is somewhat constricted, and when ready for pupation the larva suspends the bag at that end by means of a thin strand of twisted silk, and the opening is closed.

The young bags are not stalked, but are applied with the edges of their flat circular base to the leaf. The smooth, conical surface offers very little resistance to the wind, which might otherwise dislodge the bags. As an additional safeguard against such detachment, a couple of larger pieces of leaf are attached to the mouth end of the bag in such a way as to flare outward with their edges resting on the leaf, thus forming a couple of braces to steady the bag. When the bag becomes larger and stronger these braces are no longer required, and, as the bag is being added to from the mouth end, they can still be noticed as two projections, moving further away from the collar as the bag grows, becoming smaller and smaller through wear, until in the mature bag they can no longer be seen.

The bag of the full-grown caterpillar is about 12 mm. long by $2\frac{1}{4}$ mm. wide at its widest point, with abruptly rounded base and truncated tip. Bag smooth, composed of silk, with which are sometimes interwoven very small fragments of the leaves or catkins of the oak, but in most cases these particles cannot be recognised, and it appears as if the covering of the bag were made of the excrement of the larva, mixed with silk. Colour of bag grey, sometimes with an olive tinge.

The bag is attached to a branchlet or the midrib of a leaf by a cord of twisted strands of silk, 5 to 10 mm. long, the half near to the bag being covered with the same material as the bag itself (text-fig. 19, 1, κ).

The bag is lined inside with a thick, tough layer of smooth,

white silk; the neck of the bag is filled up with fluffy, loosely-woven, cream-coloured silk. At the top of the cavity we find the exuviae of the last instar of the larva.

When ready for pupation, although no inner bag is made, we find that both the upper end of the bag and the lower half are filled with a dense mass of fluffy, sticky, white silk, leaving a clear space at the middle, in which the pupa lies head downward.

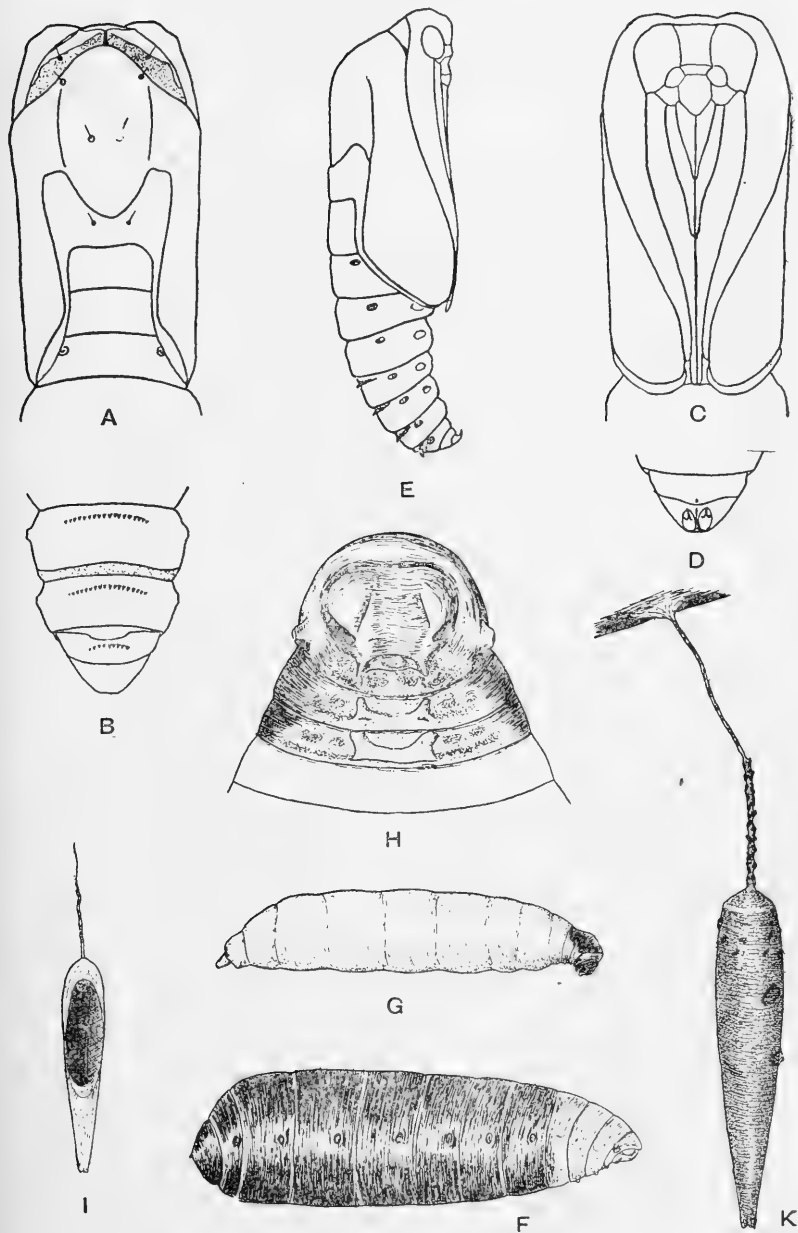
In the case of the female the exuviae of the last moult are found pushed to the upper part of the bag cavity; in the male pupa these last larval exuviae are pushed out of the bag, remaining suspended at the lower end, entangled in the silk. These exuviae are light in colour, and especially the head-case, so that here, as in the Wattle Bagworm, the last instar is one in which the caterpillar does not attain its full coloration, and, presumably, does not feed.

Male Pupa.—Length 6 mm., width 1.5 mm., depth 1.8 mm., truncated in front; sides of wing-cases nearly straight and parallel; pupa tapering rather abruptly caudally from the posterior edge of the 6th abdominal segment (text-fig. 19, A-E). Head only slightly convex; eyes large, prominent. Clypeus short, trapezoidal; paraclypeals subcircular, distinct; labium broad, large; maxillary palpi distinct, trapezoidal. Antennal cases broad, longitudinally sulcate, not reaching the end of the wing-cases. Ventral edge of front wing-cases reaching to the middle of the 3rd abdominal segment, posterior wing-cases projecting slightly beyond them on all sides. Prothorax

TEXT-FIG. 19.—*Semimanatha fumosa* Janse.

- A. Dorsal view of anterior part of male pupa. $\times 13$. B. Dorsal view of posterior part of male pupa. $\times 13$. C. Ventral view of anterior part of male pupa. $\times 13$. D. Ventral view of posterior end of male pupa. $\times 13$. E. Side view of male pupa. $\times 10$. F. Side view of female pupa, showing membranous anterior portion. $\times 7$. G. Side view of female. $\times 7$. H. Ventral view of anterior portion of female; note forked ventral process of the head and fleshy rudiments of thoracic legs. $\times 27$. I. Bag of adult female in longitudinal section, showing the upper and lower portions filled with white silk, leaving a middle cavity for the pupa. $\times 1.7$. K. Bag of full-grown larva, showing the cord with a broadened upper attachment and a lower thickened ridged portion. $\times 3$.

TEXT-FIG. 19.



declivous, slightly concave transversely. Mesothorax massive, slightly convex dorsally; metathorax longer than the 1st abdominal segment. Abd. segments 1 to 4 smooth, without spines; 5 to 8 with a short, transverse, dorsal row of small spines at the anterior edge. Cremaster rudimentary, consisting of a pair of minute, blunt, conical hooks.

Female Pupa.—Length 7 mm., width 2.5 mm., greatest width at 6th abdominal segment. Head and thorax of pupa membranous, with only a very slight amount of chitination on the dorsal aspect of the thoracic segments. First abdominal segment membranous over its anterior half; other segments normally chitinated (text-fig. 19, f). Colour of heavily chitinated parts (i.e. dorsal aspect of abdominal segments and all parts from posterior half of 5th abdominal segment caudally) black; remainder of chitinated parts Hay's brown (XXIX), dorsal aspect of membranous part cinnamon (XXIX), spiracles and leg-scars cinnamon (XXX). Surface matte. Dorsal aspect of abdominal segments transversely striate, less pronounced on 6th segment and posteriorly. Anterior, membranous part very much wrinkled, so that no details can be made out.

Adult Female.—Apterous, vermiform. Length 7 mm. Head deflected, concealed by prothorax, retractile (text-fig. 19, g). Head subquadrate; pigment spots (eyes) elongate, triangular; buccal opening transverse, oval. On each side of this the head is prolonged into a short, conical prong, those of the two sides being slightly divergent. Prothorax large, anterior part deflected; spiracles large, prominent. Thoracic segments chitinated on dorsal and lateral aspect only, ventral aspect membranous. Thoracic legs rudimentary, represented by two small membranous protuberances, those on the 3rd segment the largest and connected by a common base. Remainder of body membranous, transparent, sparsely covered with scale-like hairs. Ovipositor short, truncate, conical, membranous, apparently without supporting chitinous rods. Colour of body amber yellow (XVI), chitinated parts (exposed portion) deep chrome (III).

Female enclosed in bag and in chrysalis case, only the head and part of the thoracic segments being exposed.

Seasonal History.—Adults were found emerging on December 18th and again in January. At the former date larvæ were also found which appeared to be only three-quarters grown, therefore the period of emergence of the adults must be fairly long.

Adults bred from young larvæ collected in October emerged in December and January, so that there may be two generations a year, and there is probably a considerable overlapping of the first and second generations.

Economic Importance.—The larva is primarily a surface feeder—that is, it does not eat the entire leaf, but confines its depredations to the superficial layers, eating small patches here and there, and apparently moving about from day to day, the method of feeding being probably best described as “grazing.” These grazed patches may occur on the upper or the under surface of the leaf, and, where those of the two surfaces overlap, the leaf is entirely perforated, and we thus find on an infested tree the leaves covered with irregular skeletonised patches and scattered holes.

The damage done to the tree may be very considerable; on one tree I estimated that between one-quarter and one-third of the leaf surface was thus destroyed, and although it was in the autumn (April), the tree was in places sprouting out new foliage to replace the loss of respiratory surface. This, of course, greatly weakens the tree, and may account for the observation mentioned below, that these bagworms appear to be confined to trees of low vitality, one brood preparing the way, as it were, for that of the coming season, the same tree being re-infested from year to year.

While we have found this bagworm locally injurious to the oak, its economic importance is comparatively slight. The species is very heavily parasitised by a small hymenopteron, and, moreover, the caterpillars are subject to a fungus disease, like that of the Wattle Bagworm. For the present

these two natural agencies are entirely sufficient to check any undue increase of the species.

This bagworm seems to be extremely local in its distribution. While one tree may be heavily infested, other trees in the neighbourhood may entirely escape. It seems that the young, upon hatching, do not travel far. We first found this bagworm on a single tree adjacent to the Natal Museum, while the other neighbouring trees were free. When returning to Pietermaritzburg the next season I found that the tree had been cut down, and, to my surprise, I was not able to find the insect on any other tree, although oaks are fairly common in the town. At last I was fortunate enough to find a number of specimens on a single small tree, while other oaks surrounding the infested one were quite free from them.

The method by which this species is distributed has not been ascertained, but from the peculiarities of its distribution, as noted above, we may assume that the wind-dispersal of the young does not play such an important part as in the case of the Wattle Bagworm, although it may assist to some extent. The three methods which might be conceived to bring about this distribution are:

(A) Distribution of the Young Bagworms by the Wind.—We have observed no pronounced phototropism in a brood of newly-hatched young of this species like that seen in *A. junodi*, and accordingly the young would not travel to the top of the tree so as to be taken up by the wind. This method is also not very probable, since we have invariably found that the lower branches of the tree are most heavily infested, which would suggest that the infestation starts from below.

It must be mentioned that both trees on which the bagworms were found were not in vigorous health, and perhaps the physiological condition of the trees may have an important influence on the distribution of the insect.

(B) Distribution of the Mature Bags by the Wind.—As the bags for pupation are attached to the midrib of the leaf, they will drop to the ground and be blown about by the

wind when the leaves fall in autumn. These dry leaves will naturally gather in protected situations, and therefore especially around the bases of trees standing in such places.

(c) Distribution by Birds.—A third method which suggests itself as being the cause of this localised distribution is the carrying of the young bagworms by birds, and I am at present inclined to accept this method as the one responsible for the sporadic infestation of the oaks in Pietermaritzburg, for if distributed by the other methods mentioned we should expect more trees to be affected, but if birds are the carrying agent a sporadic distribution would result.

A tree once infested will be re-infested from year to year from the bags which hibernate on the small branches. We have found bags on the same tree which, judging by their appearance, must have been one to three years old.

9. *Monda delicatissima* Walker. Pl. XIII, figs. 18, 19.

Monda delicatissima Wlk. Cat. xxxii, p. 407, 1865.

This pretty little bagworm is not uncommon in the coastal area of Natal. The male, a delicate black and white moth (Pl. XIII, fig. 19), has been known for a long time, having been described by Walker as early as 1865 under the present name. The writer has found it at Durban and Eshowe, Zululand; Mr. K. Munroe has collected it at Barberton, Transvaal; while the Rev. Junod¹ mentions it from Delagoa in the following terms:

“ . . . qui se distingue par deux points noirs sur les ailes antérieures. L'involucre de cette espèce est garni de petites demi-sphères découpées dans des feuilles et que la chenille fixe à angle droit contre son fourreau. Celles de l'extrémité anale sont toutes petites, celles de l'extrémité céphalique sont assez grandes. Le fourreau ressemble ainsi à une petite pagode ambulante. Il est assez commun.”

While the bags (Pl. XIII, fig. 18) are fairly common at times, the moths appear to be rather scarce, owing to the high

¹ Junod, H. A., 'Bull. Soc. Neuchatel. Sc. Nat.,' vol. xxvii, p. 248, 1891-99.

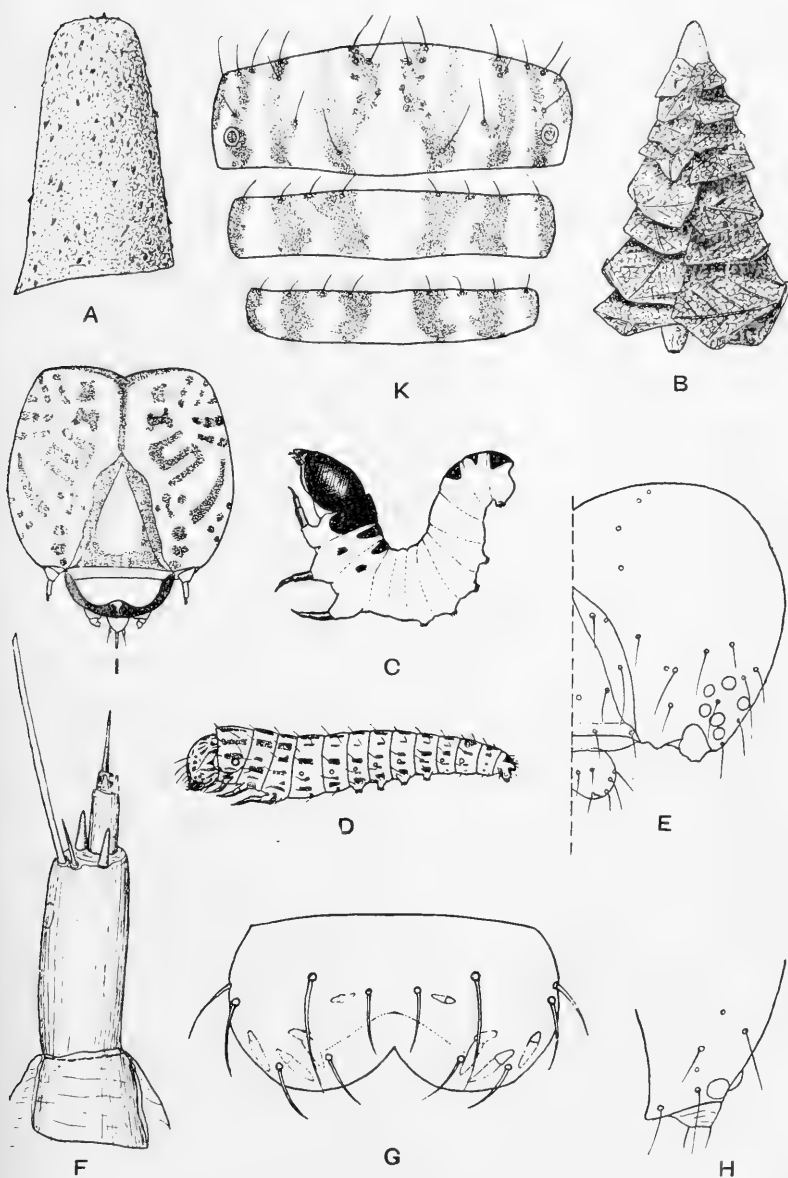
percentage of parasitised individuals and other causes. The species seems to be difficult to rear, for out of some fifty bags collected at Durban, all containing live larvæ, only five male moths were obtained and a couple of females. While this might conceivably be due to the transference of the specimens from Durban to New Hanover, Mr. Platt at Durban had no better success, and the Rev. Junod, in his article above mentioned, complains anent other species of this genus that while the bags are fairly common, it is very difficult to rear the adult.

The Bag.—This has been fittingly described by Junod as an ambulating pagoda (text-fig. 20, A, B). The bag of the fully-grown larva is about 12 mm. long, shaped somewhat like a four-sided pyramid with flaring base. It consists of an inner, cylindrical bag of white silk, to the outer surface of which are attached small pieces of the skeletonised leaf of the food-plant. These pieces are fastened to the bag by their upper edge only, and flare outward at an angle of about 45 degrees. Each succeeding piece (towards the mouth end) is larger than its predecessor, and has its end fastened to the bag underneath the projecting part of the previous one. The inside silken case is nearly cylindrical, and its cephalic end is free and movable in all directions. Looking at the bag from the mouth end, this part projects from the centre of the leafy covering like the pistil of a flower. The small size of the entire structure, the symmetrical arrangement, the skeletonised condition of the covering leaflets (making them appear like pieces of lace), all combine to give a delicate appearance to

TEXT-FIG. 20.—*Monda delicatissima* Wlk.

- A. First bag of young larva. $\times 13$. B. Bag of larva in last instar; in this example the leaves had not been skeletonised as usual. $\times 3.3$. C. Larva in first instar, showing extreme dorso-flexion of abdominal segments. $\times 13$. D. Side view of larva in last instar. $\times 7$. E. Front view of head of full-grown larva, showing setæ and ocellar area. \times . F. Antenna of larva in last instar. G. Labrum of larva in last instar, showing arrangement of setæ. \times . H. Subocellar area of larva in last instar, showing setæ. \times . I. Front of head of full-grown larva, showing pattern. $\times 13$. K. Thoracic shields of full-grown larva, showing pattern. $\times 20$.

TEXT-FIG. 20.



this bag, and the name *delicatissima* befits the little bag as well as the pretty moth which emerges from it.

Food-plants.—The only plant on which we have found the species is *Desmodium incanum* *D.C.*, a small, creeping, low-growing leguminous herb, which the late Medley Wood, of the Colonial Herbarium in Durban, pronounced an imported weed. Its original native food-plant is as yet unknown. On *Desmodium* it is locally very common: Mr. Platt and the writer found over a hundred bags within a space of about twenty yards square. Their occurrence, however, is not constant: the following season there may be hardly a single one on the same area, while a patch a hundred yards distant may contain them in great numbers.

Number of Broods in a Season.—The life-cycle of the species is not yet fully known. There is probably a considerable overlapping of broods, and most likely there is more than one generation during the season.

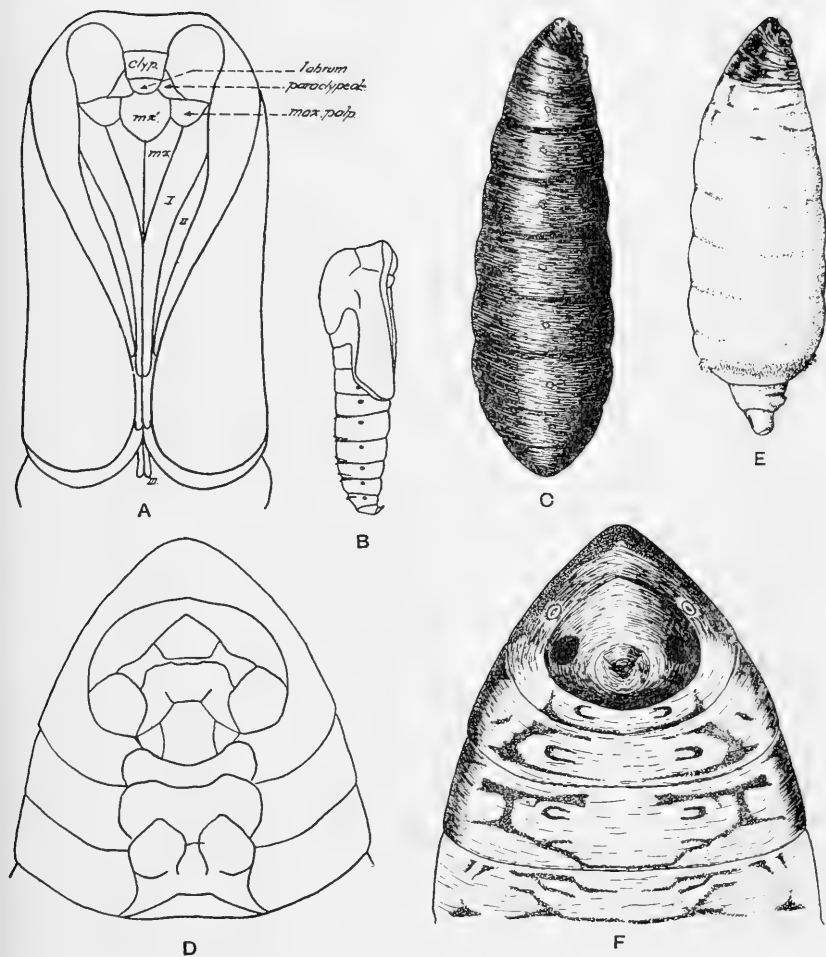
One male emerged in February, 1916, and from specimens obtained later, in March and April, the males usually make their appearance from April 25th to May 6th, but the specimen found by Mr. Munroe at Singerton, Barberton District, Transvaal, disclosed the moth in June.

In the box containing the male which emerged in February, young larvæ from another bag were also found, and, when collected at the end of March, bags of various sizes were observed. Since *Desmodium incanum* is green throughout the year at the coast, there is always food at hand for the larva, and the species breeds all the year round.

Larva.—Illustrations of the larva are given in text-fig. 20, C-K.

Male Pupa.—Length 5 mm., dark brown, shining, head and thorax turning olive-brown towards maturity. Pupa truncated in front, head deflected ventrally so that the area around clypeus, base of eyes and eye-collar forms a shallow, transverse furrow (text-fig. 21, A, B). Wing-cases reach to the posterior edge of the 3rd abdominal segment. Antennal cases long, reaching down to about three-quarters the length

TEXT-FIG. 21.

*Monda delicatissima* Wlk.

- A. Ventral view of anterior part of male pupa. $\times 35$. B. Side view of male pupa. $\times 12$. C. Side view of female pupa. $\times 12$. D. Ventral view of anterior part of female pupa. $\times 35$. E. Side view of female. $\times 12$. F. Ventral aspect of head and thorax of female. $\times 45$.

of the wing-cases. Mesothorax massive, very convex dorsally. Abdominal segments devoid of spines, but with setae corresponding to those of the larva. Cremaster apparatus consists of two hooks on broad, conical bases; hooks sharp, curved and directed cephalo-ventrally.

Labrum transverse, short, sulcate along median line, transversely striate; paraclypeals distinct, triangular, rugose. Labium large, labial lobes not distinct; maxillary palpi large, triangular. Antennal cases broad, showing pectinations of antennae, reaching to the end of the first legs. Pronotum finely transversely striated; mesonotum faintly so, very convex at median part; metanotum irregularly sulcate. Abdominal segments sulcate transversely, with membranous art (inter-segmental) large, lighter-coloured and smooth. Abdominal segments 3 to 6 with a row of minute teeth at posterior edge; abd. 4 to 8 with a dorsal row of stronger spines along anterior edge, which spines reach their greatest development on the 8th segment. On segment 9 the spiracles are prominent and situated on lateral prominences. The cremaster consists of two sharp, curved spines, the bases of which are elliptical and continuous in the median line.

Female Pupa.—Length 5.5 mm., width 1.5 mm., cylindrical; posterior part from 7th abdominal segment abruptly rounded; from the 6th abdominal segment gradually and uniformly tapering anteriorly (text-fig. 21, c, d). Colour reddish-brown. Abdominal segments smooth, with apparently a total absence of hooks, spines, and striations. Dorsal aspect of head, pro- and mesothorax finely spinulate. A very slight median carina on pro- and mesothorax. Head deflected ventrally, prothorax projecting beyond the head in front. Ventral surface of head very much wrinkled, so as to almost totally obscure the various parts. Legs indicated by a bilobed median ventral process on pro- and mesothorax, on the metathorax by two processes, united at their bases.

Adult Female.—Apterous, vermiform, cylindrical, anterior part tapering gradually from the 3rd abdominal segment anteriorly, posterior part abruptly rounded from the end of

the 7th abdominal segment. Segments 9 and 10 much narrower than the preceding segments (text-fig. 21, E, F).

Length 5 mm., width 1.8 mm. Colour of body sea-shell pink (XIV), chitinated parts of head and thorax pale yellow orange (III), with anterior margins of thoracic segments cinnamon rufous (XIV). Ventral aspect of thoracic segments marked with garnet brown (I) on anterior and posterior margin, as also the loops indicating the position of the thoracic legs.

Head small, rounded, retracted; pigmented eye-spots prominent, round, black. Anterior margin of mouth opening thickened. No mouth-parts. Prothorax conical; anterior margin inflexed, embracing head and projecting beyond it as a cone. Dorsal chitination slight, more pronounced on anterior part. Mesothorax only slightly chitinated on its dorsal part, as also the metathorax. No legs or rudiments of such can be distinguished; their places are indicated by pigmented loops with their openings medial. Abdominal segments 1 to 6 transparent, 7th segment with a fringe of very fine, cream-coloured, woolly hairs near the posterior margin. Eighth abdominal segment short, cylindrical; 9th segment conical, curved ventro-posteriorly, supported dorsally on its cephalic margin by a chitinated edge. Body-wall soft, membranous, transparent. On ventral aspect of the thoracic and abdominal segments the nerve ganglia are plainly visible.

Adult Male.—The male (Pl. XIII, fig. 19) is a pretty little moth, measuring, with wings expanded, about 18 mm. The body is dark, thorax covered with white hairs, antennæ flattened, dark grey. The wings are translucent white, the upper part of the fore wings black, each with a small black spot a little beyond the centre of the wing.

In our breeding-cages the males were commonly found in the morning, so they presumably emerge at night. Their habits, such as time and manner of flight, mating, etc., have not been observed.

For the present, the species is not of any economic impor-

tance, but it may become a pest in the flower garden on some of the leguminous ornamental plants. For the time being it is effectively held in check by its parasites.

10. *Monda major Heylaerts.*

Monda major Heyl. C.R. Soc. Ent. Belg., vol. xxxiv, p. 182, 1891 ;
Junod, Bull. Soc. Neuch. d. Sc. Nat., vol. xxvii, p. 249, 1899.

This species has been reported by Junod as being abundant at Delagoa, but I have thus far failed to find it in Natal. It does not appear to be of economic importance. The food-plant is given as *Helichrysum parviflorum Klatt.*, which, together with numerous other members of this genus, occurs abundantly in Natal, so it is quite probable that *Monda major* will be found here.

The species has been described by Heylaerts from the male only, while the Rev. Junod has described and figured the bag and furnished us with some notes on the biology of this species as follows :

“La *Monda major Heyl.*, que j’ai trouvée abondante sur cette Composée, a un fourreau sphérique formé de brindilles plus ou moins recouvertes et noyées dans un tissu de soie blanche. Celui du mâle paraît moins garni de ce tissu que celui de la femelle. J’ai cru remarquer aussi que la chenille du mâle se transformait en chrysalide dans un cocon intérieur qu’il se faisait à la manière de l’*E. junodi*. La femelle après son éclosion ne sort pas les trois premiers anneaux du cocon. Elle reste dans son fourreau dont elle brise seulement l’extrémité pour permettre au mâle de la féconder.

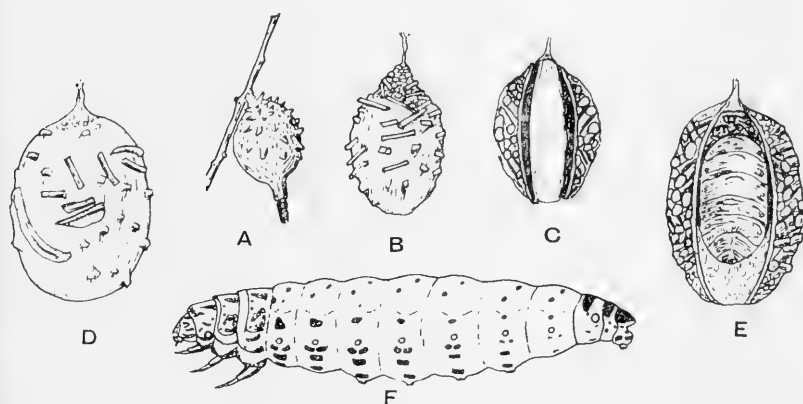
“Un fait de mimétique intéressant à signaler c’est que ces fourreaux de femelle, si abondamment revêtus de soie grisâtre, ressemblent extrêmement à certains bourgeons avortés et desséchés de l’*Helichrysum parviflorum*, et il faut avoir un œil exercé pour les en distinguer.”

The female and immature stages have not been described.

Male Bag.—The full-grown bag of the male is about 12 mm. long by 7 mm. wide, the middle part spherical, with the upper end, by which attached, pointed, and the lower end somewhat flattened (text-fig. 22, D, E). It consists of an oval case of silk, to which are attached small pieces of midrib, and probably also of the flower-stalk of the food-plant,

Helichrysum parviflorum. These are attached crosswise, at right angles to the long axis of the bag. These sticks being longest at the middle part of the bag, and both ends being without them, the outer contour of the bag is rendered somewhat spherical. This appearance is accentuated by the lower two-thirds of the bag being covered with a layer of silk, covering the little twigs so as to leave only the points exposed.

TEXT-FIG. 22.



Monda major Heylaerts.

- A. Bag from which moth has emerged. $\times 0.9$ (after Junod). B. External view of male bag. $\times 1.8$. C. Male bag in vertical section, showing cocoon. $\times 1.8$. D. Female bag in pupation stage. $\times 1.8$. E. Female bag in vertical section, showing pupa. $\times 1.8$. F. Full-grown female larva (setæ not showing). $\times 4$.

When pupation time approaches, the male spins a cocoon in the form of an inner column of silk, attached to the upper and lower end of the bag but free in the middle.

Female Bag.—This is considerably larger than that of the male (text-fig. 22, D, E). It averages 16 mm. in length by 10 mm. in width; is more oval in shape, with both ends truncated. The construction of the bag is the same as that of the male, with the exception that the outer webbing covers nearly the entire bag, leaving only the neck (upper part) free.

When pupating no inner bag is made, but the space between the pupa and the lower end of the bag is filled with fluffy, white silk.

The bags greatly resemble the dried flowers of the food-plant; these are also very woolly and white, while the points of the leaflets forming the involucre project through the woolly covering. The dried flower droops on the stem, and as the calyx (now the upper end) is less woolly than the flower part, this heightens the resemblance between it and the bag of *Monda major*. As already mentioned by the Rev. Junod, it is very difficult to distinguish the bags on the food-plant.

Larva.—A full-grown female larva is illustrated in text-fig. 22, F. Length 15 mm. (female), thickness 3.5 mm., greatest thickness at the 3rd abdominal segment. General colour of body ivory yellow (XXX), head cream buff (XXX), markings on head, thorax and body mummy brown (XV).

Width of head-case 1.8 mm. Markings of head and thoracic plates of the usual bagworm pattern, i.e. radially arranged spots on the parietals and longitudinal stripes with scattered dots on the thoracic plates. Abdominal segments with small mummy brown chitinous plates bearing the body setæ. On abd. 8, 9, and 10 there is a conspicuous large, median dorsal plate. On abd. 1 and 2 these setiferous plates are larger and more conspicuous than on the other segments.

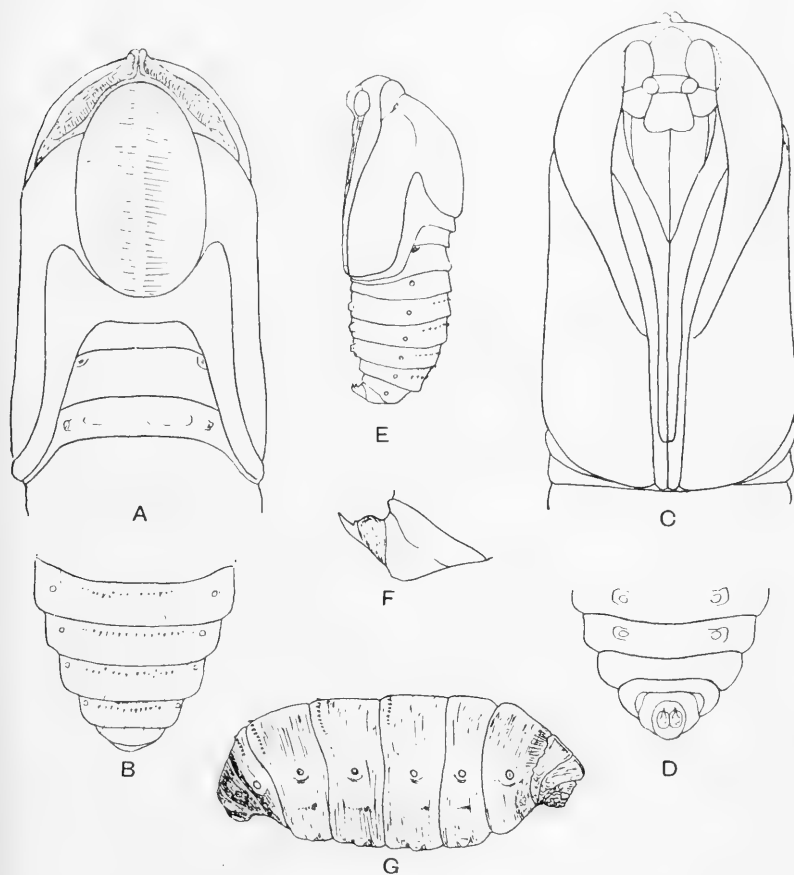
Number of hooklets on prolegs are as follows :

Side.	Abd. 1.	Abd. 4.	Abd. 5.	Abd. 6.	Anal.
Right .	22	20	22	18	18
Left .	22	16	22	22	18

Male Pupa.—Length 6.5 mm., width 2.5 mm.; greatest width at the 3rd abdominal segment; depth 2.2 mm., greatest depth at metathorax and at the 4th abdominal segment. Area across the ends of the maxillary palpi forms a transverse shallow groove (text-fig. 23, A-F). Wing-cases reach to the

posterior edge of the 3rd abdominal segment. Head rounded, smooth. Clypeus transverse, trapezoidal, paraclypeals distinct,

TEXT-FIG. 23.



Monda major Heylaerts. Pupa.

- A. Dorsal view of anterior part of male pupa. $\times 13$. B. Dorsal view of posterior part of male pupa. $\times 13$. C. Ventral view of anterior part of male pupa. $\times 13$. D. Ventral view of posterior part of male pupa. $\times 13$. E. Side view of male pupa. $\times 7$. F. Side view of posterior extremity of male pupa. G. Side view of female pupa. $\times 5.3$.

rounded, rugose. Labrum large, trapezoidal, maxillary palpi distinct. Antennal cases broad, flattened, the basal portion

partly covering the eyes; the antennal cases reach to the level of the 2nd abdominal segment. Second leg-cases long, reaching almost as far down as the 3rd pair, which reach nearly to the edge of the wing-cases. Prothorax with a double median convex carina, the surface longitudinally sulcate on the posterior half. Mesothorax massive, strongly convex, with a faint median carina and finely transversely striate, especially on the anterior half. Humeral area deeply sulcate. Metanotum rugose, hind wing-case visible to beyond the lateral angle of the front wing-cases. Area of 1st abdominal segment depressed. Remaining abd. segments 2 to 7 dorsally with transverse, lateral depression, having a median area and posterior margin projecting. Abd. segments 4 to 7 with a short transverse row of rudimentary teeth near the anterior edge, more strongly pronounced on the 7th, where the posterior margin of the 6th is also finely denticulate over a corresponding distance. On the ventral surface the scars of the abdominal prolegs are prominent, slightly protruding. Cremaster consists of two curved hooks, directed ventro-anteriorly, on broad bases, flattened laterally.

Female Pupa.—Plump, vermiform, subcylindrical, attenuated posteriorly from the anterior edge of the 3rd abdominal segment and anteriorly from the posterior edge of the 6th abdominal segment (text-fig. 23, g). Head and ventral part of thoracic and 1st abdominal segment strongly wrinkled, so that no head parts or thoracic legs can be distinguished. Dorsal aspect of thorax with a weak median carina, and finely striated transversely, that of the 1st abdominal without carina and striated longitudinally. Other abdominal segments smooth, scars of prolegs projecting. A dorsal row of minute rudimentary teeth on the posterior edge of 4th to 7th abdominal segments, the remaining segments smooth. No trace of cremaster armament.

Length 9 mm., diameter 4 mm. Colour of abd. segments 2 to 7 ochraceous orange (XV), head, thorax, and abd. 1 tawny (XV), with bronze sheen, caudal segments russet (XV).

11. *Monda rogenhofferi Heylaerts*. Pl. XIII, figs. 20, 21.

The "Turret Bagworm."

Monda rogenhofferi Heyl. C.R. Soc. Ent. Belg., vol. xxxiv, p. 182, 1891; Kirby, Cat., p. 518; Junod, Bull. d. l. Soc. Neuch. d. Sc. Nat., vol. xxvii, p. 250, 1899.

The bag of this pretty little species greatly resembles that of *Monda major*, but is smaller, more pointed, and differently constructed (Pl. XIII, fig. 20). It has been reported from Delagoa by the Rev. Junod, in the following terms :

"Le fourreau de cette espèce est plus petite encore (que *M. delicatissima*) et se compose de bouts de bois entassés en pyramide autour du sac intérieur. L'image est blanc aussi avec une suffusion de noir sur les ailes antérieures."

In Natal this bagworm appears to be rare, and only twice has a bag of this species been sent to me—the first collected by Mr. Janse, in Stella Bush, Durban, the second by Mr. Platt, from the same locality. Both were males. The first one disclosed the moth in February; the second was an empty bag from which the male had emerged.

The life-history, immature stages, female moth, food-plants, and number of generations are unknown.

The Bag.—The following description is based on an empty bag from which the male had escaped (text-fig. 24, A, B) :

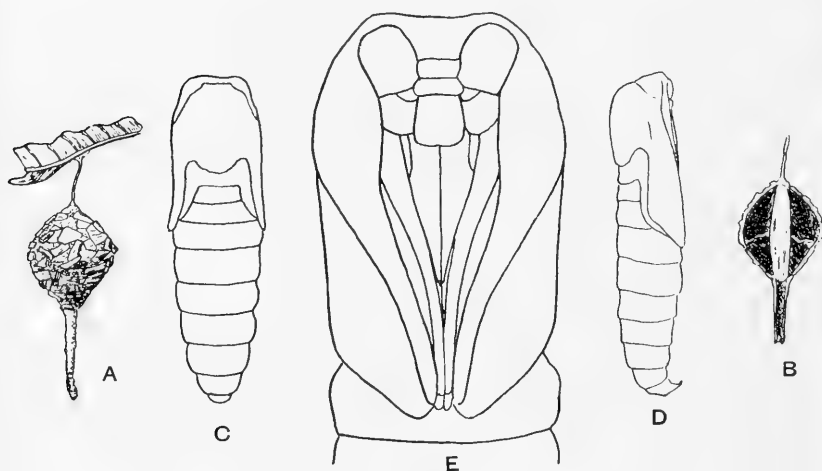
Length of bag 13 mm., width 6 mm., consisting of two parts—an upper, almost spherical (the bag itself), and a long, slender neck. The rounded part consists of a very thin layer of silk, to which are attached small pieces of leaf, irregular in shape and direction, which are fastened down over practically their entire surface so as to conform to the rounded outline of the bag. The majority of these are attached horizontally or obliquely; none were found directed vertically. On the neck part these covering pieces are lacking; only some minute particles are found interwoven with the silk.

Inside this case we find a narrow, cylindrical inner bag, extending as a continuation of the neck to the upper end and slightly wider in the middle. This inner bag, which reminds one of that made by *A. junodi*, extends like a cylindrical

column through the centre of the bag and is supported by two radial strands of silk, which run from its circumference to the wall of the outer bag.

Male Pupa.—Length 5 mm. General colour raw sienna (III), head, thorax, and wing-cases brussels brown (III). Dorsal aspect dull, ventral aspect and wing-cases shiny.

TEXT-FIG. 24.



Monda rogenhofferi Heylaerts.

- A. Bag of full-grown larva. $\times 1.7$. B. Bag opened vertically to show inner bag (cocoon) supported by two bands to the inner wall of the outer bag. $\times 1.7$. C. Dorsal view of male pupa. $\times 9$. D. Side view of male pupa. $\times 9$. E. Ventral aspect of head and thorax of male pupa. $\times 27$.

Head slightly projecting ventrally, eyes large, prominent (text-fig. 24, C-E). Clypeus quadrate, convex. Labrum transverse, short, distal margin slightly concave, paraclypeals distinct, partly concealed by the lateral corners of the labrum. Labium large, broadened distally, maxillary palpi large. Antennæ broadened, transversely sulcate over their entire length. Wing-cases reaching ventrally to nearly the posterior edge of the 3rd abdominal segment. Abdominal segments on ventral aspect unarmed, finely striated transversely. Pro-

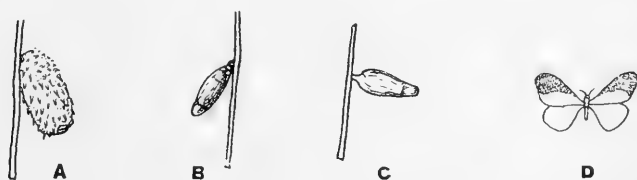
thorax small, punctulate. Mesothorax large, striato-punctulate, humeral angles broadly rounded. Metathorax narrow, posterior wing-cases visible to the anterior half of 3rd abdominal segment. Abdominal segments finely striated transversely, 1 to 3 unarmed; 4 and 5 with a row of minute hooks on posterior declivity; 6, 7 and 8 with one row of stouter hooks near cephalic edge, strongest and most numerous on the 7th segment; segment 9 unarmed; segment 10 bears a well-developed cremaster, consisting of two stout, curved hooks on laterally compressed, conical bases, and directed ventro-anteriorly.

12. *Monda heylaertsi* Junod.

Monda heylaertsi Junod. Bull. de l. Soc. Neuch. d. Sc. Nat., vol. xxvii, p. 250, 1899.

This species, apparently the smallest of the four species here enumerated, has been described by Junod from Lake

TEXT-FIG. 25.



Monda heylaertsi Junod.

A. Bag of mature larva. B, C. Bags of young larva. D. Male moth. All nat. size. (After Junod.)

Rikatla, Delagoa. I have not found the species in Natal, and do not know of a specimen in any of the collections in South Africa. Junod's description is translated as follows:

Wing expanse 13 mm. White, with front wings for the greater part grey. Fore wings white, transparent at base, with a uniform light grey diffusion, which extends over the greater part of the wing, leaving white only as a narrow region of triangular shape, running from the middle of the anterior border at the costa to 1 mm. from the base (text-fig. 25, D). Posterior wings uniformly white and trans-

parent. It is distinguished by its small size (*Monda major* measures 16 mm., *M. rogenhofferi* 14 mm.), and by the uniform grey diffusion. *M. major* is entirely white; *M. rogenhofferi* has a smaller diffusion, and *M. delicatissima* has two black spots on the fore wings.

The species has been described from the male moth only; the immature stages and female are unknown.

Junod gives the following description of the bag (text-fig. 25, A-C):

“Mais ce qu'il y a de plus caractéristique dans cette espèce minuscule, c'est son fourreau. Il est cylindrique, à 8 mm. de long et est tout hérissé de très petits poils ressemblant à de courts cheveux brun-gris pris évidemment à des épillets de graminées. Les petites chenilles, en sortant du fourreau au fond duquel la mère a déposé ses œufs, tondent probablement ces involucres, y enlèvent tous les poils, car on les retrouve absolument nus quelque temps après.

“J'ai découvert cette espèce dans la dépression actuellement envahie par le lac de Rikatla.”

EXPLANATION OF PLATE XIII,

Illustrating Mr. C. B. Hardenberg's paper, “South African Bagworms,” Part II.

Acanthopsyche tristis Janse.

FIG. 1.—Nat. size. The larger bag is covered with grass, while the smaller bag on the right is attached to *Acacia* sp. and has some of the leaves fixed to the bag.

FIGS. 2, 3.—Nat. size. Bags covered with pieces of grass.

FIGS. 4, 5.—Nat. size. Bags provided with many wattle leaves.

FIG. 6.—Nat. size. The inner silk bag is exposed owing to the pieces of grass being worn away.

FIG. 7.—Nat. size. Male moth.

Acanthopsyche alba Janse.

FIG. 8.—Nat. size. Bag.

Clania moddermanni (Heyl).

FIG. 9.—Nat. size. Bags covered with small sticks.

FIG. 10.—Nat. size. Bag covered with thorn spines.

FIG. 11.—Nat. size. Male bag.

FIG. 12.—Nat. size. Bag provided with both small sticks and thorn spines.

FIG. 13.—Nat. size. Female bag with extruding silk strand.

FIG. 14.—Nat. size. Male moth.

Manatha æthiops Hmps.

FIG. 15.— $\times 3$. Male bag.

Manatha sp. (Gibson's Bagworm).

FIG. 16.—Nat. size. Bags in situ.

Semimanatha fumosa Janse.

FIG. 17.— $\times 3$. Male moth.

Monda delicatissima Wlk.

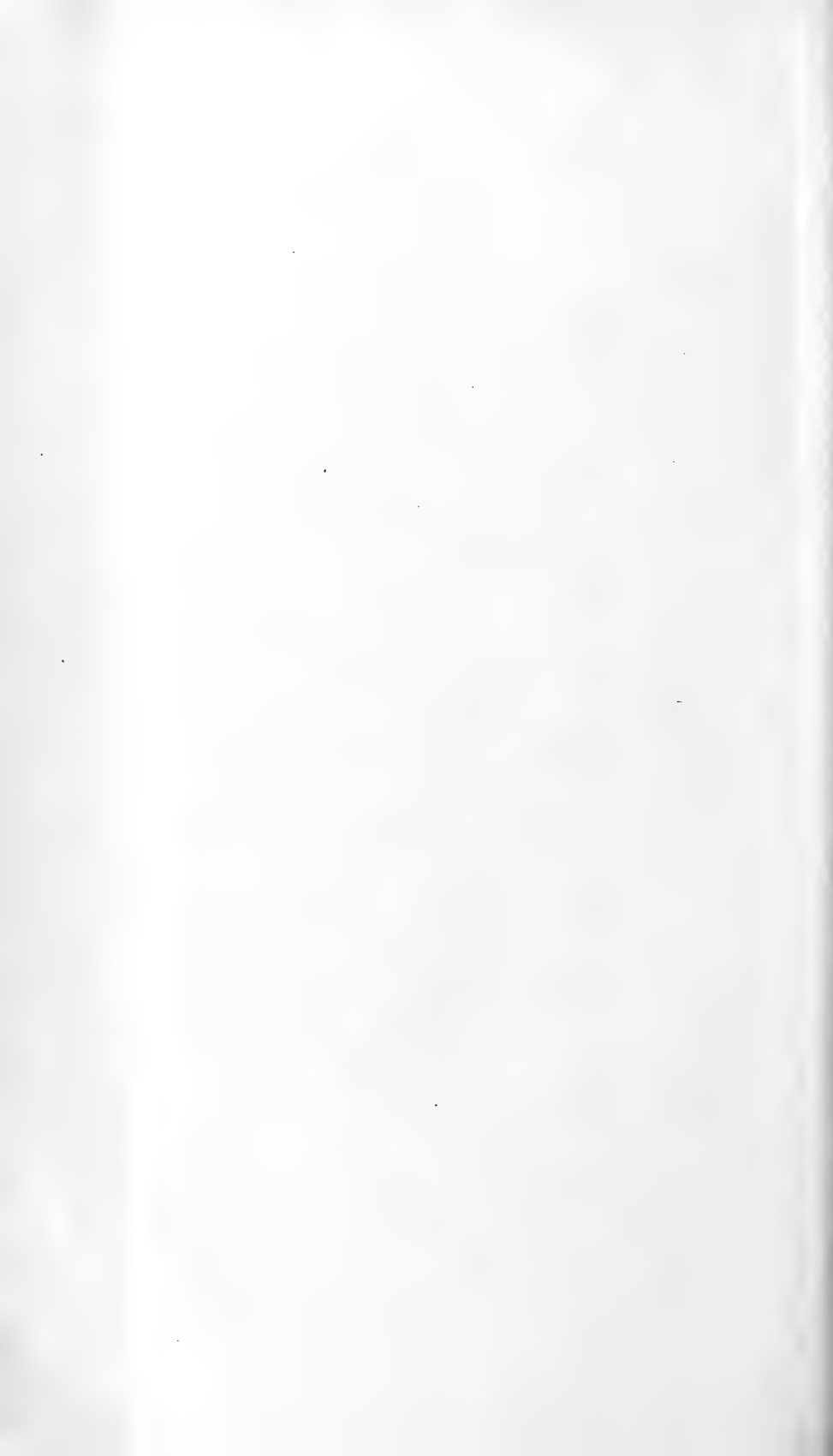
FIG. 18.— $\times 3$. Bag.

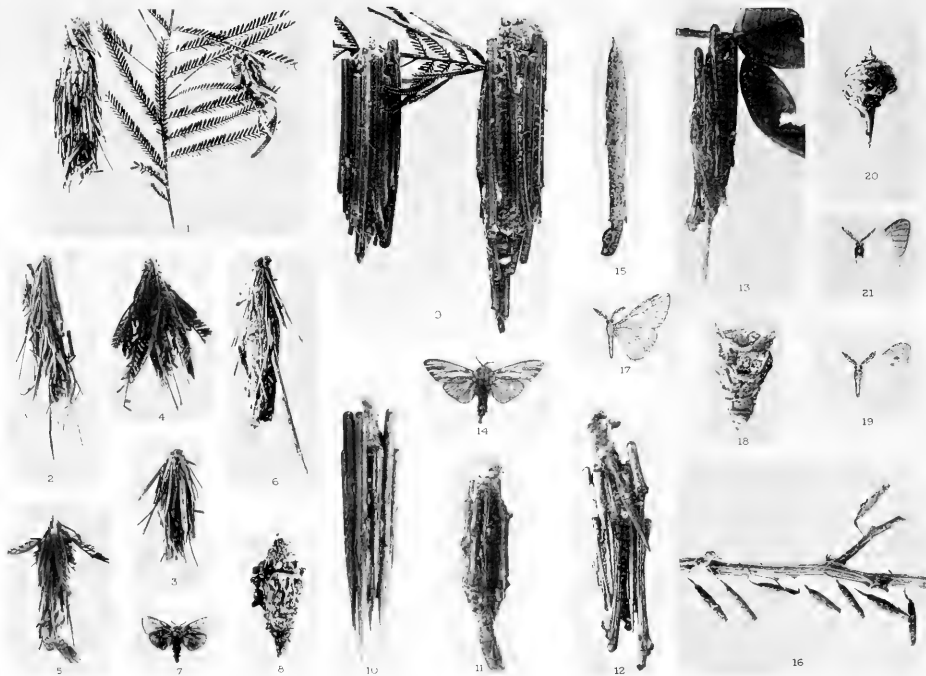
FIG. 19.— $\times 3$. Male moth.

Monda rogenhofferi Heyl.

FIG. 20.— $\times 3$. Bag.

FIG. 21.— $\times 3$. Male moth.





SOUTH AFRICAN BAGWORMS

Acanthopsyche tristis Jans., figs. 1-7. *Acanthopsyche alba* Jans., fig. 8. *Clania maddermanni* (Hagl.), figs. 9-11. *Manatha aethiops* Hagl., fig. 12. *Manatha* sp., fig. 13. *Semimanatha fumosa* Jans., fig. 17. *Monda delatissima* Hagl., figs. 18, 19. *Monda torenhofferi* Hagl., figs. 20, 21.



Contributions to a Knowledge of the Terrestrial Isopoda of Natal.

Part II.

By

Walter E. Collinge, D.Sc., F.L.S., etc.,

Carnegie Fellow, and Research Fellow of the University of St. Andrews.

With Plate XIV.

THE peculiar and interesting genus here described was discovered by Dr. Conrad Akerman at Umhlali, Natal, in May, 1916, and I have much pleasure in associating with it his name as a slight appreciation of his indefatigable energy and labours in connection with the elucidation of the Terrestrial Isopoda of Natal.

There are a number of characters which separate the genus *Akermania* from any hitherto described, not the least striking being the shape of the cephalon, the folded coxopodite beneath the pleural plates of the 1st mesosomatic segment, the feeble walking legs on segments 2—7, the short expanded uropoda with their characteristic setæ, and the shape of the telson.

As to the relationship with other genera, it is somewhat difficult to place this new genus. The oral appendages afford no assistance. In all probability it belongs to the *Cubaridæ*, but it is widely separated from *Cubaris Brandt*, or any of the allied genera.

AKERMANIA gen. nov.

Body oblong oval, strongly convex, richly setose or spiny; scales large and definite, variable in shape. Cephalon without lateral or median lobes; anterior and posterior margins distinct; epistome almost flat. Eyes compound, ocelli large, situated dorso-laterally. Antennulæ absent. Antennæ very short; flagellum 2-jointed. Coxopodite of the 1st and 2nd mesosomatic segments folded to form a groove and ridge beneath the pleural plates. Appendages of the mesosome feebly developed. Uropoda short and small, not extending beyond the telson, thick, strongly-raised, and convex; exopodite small, situated in a groove on the lower inner margin of the basipodite. Telson ovally expanded anteriorly, broader than long, posterior margin almost truncate.

This genus differs from *Cubaris Brandt* in the form of the cephalon, the absence of antennulæ, in the feeble development of the mesosomatic appendages, and in the form of the telson and uropoda. Further, in the great development of the spines, setæ, and scales, it differs from any other genus of the family Cubaridæ.

Akermania spinosa sp. n. Pl. XIV, figs. 1-12.

Body oblong oval, strongly convex, with numerous bluntly-ending spines and short setæ with bulbous bases, on the cephalon and mesosomatic segments; on the metasomatic segments the spines are fewer (fig. 1). Cephalon (fig. 2) without lateral or median lobes; anterior and posterior margins distinct, anterior margin with tooth-like spines; epistome almost flat. Eyes fairly large, compound, with large ocelli, situated dorso-laterally. Antennulæ absent. Antennæ (fig. 3) short, setose; flagellum 2-jointed, the distal joint being slightly more than twice the length of the proximal one, with terminal setose style. First maxillæ (fig. 4), outer lobe terminating in four stout, incurved spines and six smaller, straighter ones; inner lobe narrow, with two equal-sized setose spines. Second maxillæ (fig. 4) thin and plate-like, terminating distally in a

setaceous lobe on the inner side. Maxillipedes (fig. 6) with broad basal plate; terminal joint of the outer palp multi-spinous, with single spine on the middle joint and two stout ones on the inner border of the first joint; the inner palp is rounded terminally, and has three prominent spines. The segments of the mesosome (fig. 7) are strongly arched, and have two transverse rows of spines. The coxopodite of the first segment forms a deep groove beneath the pleural plate (fig. 8), into which the coxopodite of the second segment fits. Mesosomatic appendages 2 to 8 (fig. 10) feebly developed, sparsely setose. Metasomatic segments similar to those of the mesosome, but smaller. Uropoda (fig. 12) short and small, not extending beyond the telson; basal plate with prominent diagonal ridge, setose, thick, strongly raised, and convex; posterior margin obtusely rounded; antero-dorsal surface expanded and concave; exopodite short, and situated in a groove on the lower inner margin of the basal plate; endopodite small, setose, with terminal spine, articulating on the anterior and inner border of the basal plate. Telson (fig. 11) ovally expanded anteriorly, with posterior portion with straight sides; there are two short, broad, obtusely-pointed spines at the posterior of the expanded region; terminal margin truncate, broader than long.

Length (of largest specimen) 4.5 mm.

Colour (in alcohol) creamy-white, with numerous irregular, dark sepia-brown markings.

Habitat.—Umhlali, Winkle Spruit, Natal. (C. Akerman.)

Type.—In the Natal Museum.

The external spines, setæ, and scales in this species are of considerable interest, and would well repay further investigation. In view of the small number of perfect specimens so far obtained, I have not felt justified in making this investigation beyond utilising the specimen dissected for the appendages, etc.

The spines on the cephalon are represented by three distinct types (fig. 9, *a-c*), probably stages in the development, *a* being the perfect spine, *b* the worn-out spine with

the developing one within, and *c* a later stage, in which part of both the *a* and *b* stages are present. There are a number of lateral setæ given off from these spines in all stages. Whether or not this represents an incipient ecdysis or a condition in which the new spine, previous to a general ecdysis, is found within the old one, I am unable to say. On the dorsum of the mesosomatic segments the spines are very similar, but the edges of all the segments show numerous peculiar setæ. On the metasome the spines are shorter and stouter (fig. 11). On the antennæ, and the appendages of segments 2-8 of the mesosome, the spines and setæ are not abundant; they are of the usual character, but those towards the distal portion of the uropoda are more like those on the meso- and metasome.

Between the large spines of the mesosomatic segments there are distributed two sets of setæ which both arise from small bulbous bodies (fig. 7); the larger of the two show an indentation at their apex from which a short hair-like seta arises (fig. 13), whilst in the smaller ones two or three setæ arise from the summit.

The whole of the body and appendages are covered with a series of prominent scales varying in shape in different regions (figs. 8, 12 and 14), and a series of fine thread-like setæ.

I have been unable to find any antennulæ, and believe that they are absent.

The cephalon is strongly arched, and has three transverse rows of spines, whereas there are only two rows on the segments of the mesosome and a single row on those of the metasome.

The oral appendages do not call for any special mention. All the appendages of the mesosome are feebly developed.

The uropoda are small, and do not extend beyond the telson. The basipodite is a thickened plate, triangular in section, with a prominent diagonal ridge, formed partly by a slight elevation of the plate in this region, and partly by four rows of scales; towards the inner margin the scales become lanceolate in shape and overlap, and partly surround

the small exopodite; the posterior margin is almost truncate, whilst anteriorly the margin of each side is strongly raised, leaving a deep concavity between the two; the endopodite is club-shaped, setose, and has a long terminal spine in addition to other smaller ones.

EXPLANATION OF PLATE XIV,

Illustrating Dr. Walter E. Collinge's paper, "Contributions to a Knowledge of the Terrestrial Isopoda of Natal," Part II.

Akermania spinosa gen. et sp. nov.

FIG. 1.— $\times 12$. Dorsal view.

FIG. 2.—Anterior view of the cephalon.

FIG. 3.— $\times 84$. Left antenna, dorsal view.

FIG. 4.— $\times 230$. Terminal portion of the inner and outer lobes of the left 1st maxilla, ventral view.

FIG. 5.—Terminal portion of the left 2nd maxilla, ventral view.

FIG. 6.— $\times 220$. Terminal portion of the left maxilliped, ventral view.

FIG. 7.— $\times 36$. First segment of the mesosome, anterior view.

FIG. 8.—Underside of the lateral margin of the 1st mesosomatic segment.

FIG. 9.—Spines from the mesosome.

FIG. 10.— $\times 56$. Appendage of the 1st free segment of the mesosome.

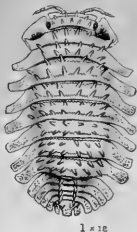
FIG. 11.—Dorsal view of the telson and last metasomatic segment.

FIG. 12.—Dorsal view of the left uropod.

FIG. 13.—Bulbous body bearing a hair-like seta.

FIG. 14.— $\times 320$. Overlapping scales on mesosomatic segments.

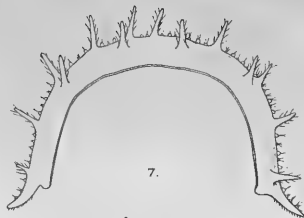
The author desires to thank the Carnegie Trust for the Universities of Scotland for a grant to defray artists' charges.



1 x 10



4.



7.



2.



13.



5.



14.



a

b

c

9.



11.



3.



6.



10.



8.



12.

S.R.K. ex E.B.B. del.

Hob, London

AKERMANIA SPINOSA, *gen. et sp. nov.*

Studies on the Post-embryonic Development of the Antennæ of Termites.

By

Claude Fuller,

Division of Entomology, Pretoria.

(Being an amplification of a paper read before the South African
Biological Society, April 18th, 1918.)

With Plate XV, and 14 Text-figures.

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SYNOPSIS.

THE study of the post-embryonic development of the antenna in South African termites has proved to be one of peculiar difficulty, and it is considered that a preliminary statement of the main conclusions will be of assistance in the subsequent discussion of the facts.

1. The antennæ of all termites are fundamentally composed of two sections—a two-jointed scape supporting a flagellum of a variable number of joints.

2. In a developing antenna the flagellum is subdivided into three zones—an apical, an intermediate and a basal. The apical zone comprises a series of joints in a somewhat well-developed stage, the more basal of the series intergrading with the intermediate zone. The intermediate zone comprises juvenile joints which are more rudimentary in character as they approach the basal. The basal zone is represented by the conventional joint III; this may be spoken of as the formative zone.

3. The post-embryonic stages are represented by a simultaneous external and internal metamorphosis, and, owing to the transparency of the organs, both phases are often discernible.

4. The internal metamorphosis is ordinarily in evidence within the conventional joint III. This joint is a capsule containing a series of variously developed joint-elements which arise by a process of proliferation taking place in front of joint II—i. e. at the apex of the scape.

5. In all species and castes examined, joint III of the antenna in its final form exists as a capsule enclosing a series of joint-elements, and, therefore, all such antennae are to be regarded as essentially arrested organs, even in the adults.

6. On hatching from the egg the development of the antenna generally reaches an external phase of X or XII joints, according to the species.

7. The final number of joints is due to the abjunction of many or few new joints in an acrogenous manner from joint III.

8. The process of joint-multiplication ceases during or before the fourth instar.

9. The mode of increase in the number of the joints is the same in all species except in *Hodotermes*. Typically two joints are abjoined from joint III periodically, so that all new joints are arranged in pairs—i. e. as sister-joints.

10. All odd-jointed antennae developing by the common mode originate either from the fusion of sister-joints when in the elemental stage before abjunction, or by the non-abjunction from III of the more proximal of such a pair.

11. The length of joint III in the final organ is dependent upon the stage of development of the joint-elements and the number of these contained within it when the process of multiplication ceases.

12. The soldiers and workers of a termite community have a curtailed development and pass through fewer stadia of growth than do their corresponding imagos.

13. In the evolution of termites a new factor arose—the building up of a food reserve—and the comparatively early subsidence of joint multiplication in the antennae of the imagos probably had its first cause in this.

14. The tendency of termites to specialise into various castes by the differentiation and reduction of parts or of the whole body also influences the post-embryonic development of the antennae, in that—

- (1) Soldiers tend to have fewer joints than their corresponding workers.



- (2) The smaller castes of a species have fewer joints than the larger.
- (3) The smaller species of termites tend to have fewer joints in the antenna than larger species to which they bear a congeneric relationship.

15. The variability of the jointing of the antenna is traceable to—

- (1) A newer tendency to be few-jointed as opposed to the primitive condition of being many-jointed.
- (2) The fusing of joint-elements, leading to the abjunction of compound joints.
- (3) Nutrition—e. g. the well-fed individual tends to be larger and have more joints in its antenna.
- (4) A probable correlation between the growth of the antenna and the development or degeneration of the sexual organs in the infertile castes.

16. The hereditary and environmental influences affecting joint formation and the general growth of the antenna are so complex, that the number of joints and their relative length and shape have scarcely any taxonomic value without a peculiarly thorough investigation of the species in all its castes and through all the successive phases of its communal development, from the state of being an incipient colony to the state of being a populous and prosperous community throwing off with much regularity swarms of winged males and females.

PART I: GENERAL REVIEW.

1. INTRODUCTION.

As with most insects, so with Termites, the antennæ are considered as possessing characters of special taxonomic value. The number of joints composing the organ of this or that caste is invariably cited as important, although for many species a certain amount of diversity is recognised. Unfortunately the tendency for the number to vary is not always taken into

consideration in species-building, and cases might be mentioned where a disagreement of one joint has been regarded as sufficient to distinguish two otherwise similar insects. Such species must be accepted with considerable reservation. In some groups the validity of a species may rest upon the relative length of one joint to another or perchance upon the ratio of the length and the diameter of certain joints; these criteria are fraught with error. Perhaps the most trying point of a diagnosis is reached when the author deals with joint III, comparing its length with that of II or IV as, fancy free, the eccentricity of the moment dictates. It is this joint III—the elusive and misunderstood section of the termite antenna—which is responsible for the present attempt to show how the joints develop, how departures may and do arise within a species and a caste, and how such may be homologised or understood.

Any description of the antenna, particularly that of the soldier, must long remain suspect and must be indefinitely tested. Later, some account is given of certain soldiers of *Termes bellicosus* with XVII-, XVIII- and XIX-jointed antennæ, all being normal developments. Of African termites, none has been more often the subject of reference than this and none has been recorded from a greater number of localities. Of its five castes, none has been more frequently before the specialist than the major soldier, but never has this been recorded as exhibiting an antenna of more or less than XVII joints. Indeed, were one asked to select a species which might, on good grounds, be regarded as having antennæ fixed in character, *Termes bellicosus* would be it. And yet one nest-series of this great mound-builder was obtained in the district of Lourenço Marques, of which as many of the major soldiers had antennæ of XVIII or XIX as had the usual XVII joints.

Fundamentally all termite antennæ are built up of elements, and these are expressed as articulated segments except when two or more unite in part or completely to form compound joints. Such joints may be noticeably compound or they may

appear simple in structure. Ordinarily the compound nature of a joint can be demonstrated; at times the condition may only be inferred.

In the different castes of a given species there is a more or less decided difference in the number of joints. It is surprising that these differences have excited practically no comment, nor have led to any serious effort being made to explain them. They seem to have been regarded as incidental to polymorphism, but an explanation cannot be offered without a comprehensive knowledge of the ontogeny of the insect antenna.

To me these termite organs are more than remarkable. The degree to which they reflect the hereditary and environmental action on the creature is a feature found in no other appendage. During the course of growth they are subject to the influence of inherited tendencies which are reacted upon by the vicissitudes in the life of the individual. If the organism is dwarfed by indifferent nutrition its antennæ are dwarfed and of fewer joints; if the opposite condition obtains the antennæ may be composed of more joints than usual. If the individual is arrested by other than nutritive factors, so also are its antennæ; if it is subject to deviation, as the production of a soldier, so also may the antennæ be modified more or less in accordance with the extent thereof. With certain exceptions and details, not calling for recapitulation here, the form of specialisation exhibited by termites is one of reduction. The socially higher forms of termites have been described as the most degenerate, but this is so only in that sense in which man is also degenerate. It is curious to reflect that the smaller the species the more it is specialised among its congeners, and that the most specialised termites are small ones. In short, all the evidence goes to show that termites have been evolved from larger insects and reduction of bulk has been one of the main lines of specialisation. The principal evidence of specialisation by reduction is, however, to be seen in the loss of a tarsal joint, in the loss of the pulvillus, in the atrophy of the abdominal appendages, in the

reduction in the number and also the degree of rigidity of the wing-ribs, and, lastly, in the ontogeny of the spiracles.

It is small wonder, then, that the antennæ should specialise along a similar route, and it is not too much to say that these organs in the higher termites tend to depart less and less from their larval condition. Inferentially the ancestral type was a multi-jointed organ with a process of joint-multiplication which was indeterminate in the sense that it continued until the general growth of the whole body had ceased. In any given species the variation in the action of the reducing factor on the ancestral tendency for an indeterminate number of joints causes the variation observable in the number of joints in the final form of the antenna. The flagellum of every antenna is an arrested structure, wherein, however regular and however small the quota of joints, extra elemental joints are present in the formative zone when the joint-multiplication subsides.

The dwarfing of an individual has a considerable effect upon the antenna, as then either fewer elements are present or those present are expressed as fewer joints. Moreover, in a given community, as the larger individuals of a caste tend to have more joints in their antennæ, nutrition seems to play an important rôle in joint production—or, to be more precise, in the development of articulations.

NANISM.—The term "nanism" is used in a restricted sense to signify the dwarfed condition of an assemblage of soldiers and workers—the characteristic state of such incipient and juvenile communities as I have examined. In any communities embracing major and minor castes dwarfing prevails to a marked degree, as the minors are little else than undersized or abridged forms of the majors. True, with a few species there are somewhat radical distinctions, but these are exceptional and offset by others where the members of a caste intergrade in size and character from small to large. Here there may be a greater difference between the largest and the smallest than exists in species where the cleavage is sharply defined. Although it still remains to be proved for all

species, it seems to me highly probable that the members of communities which have not reached the stage of reproductivity, represented by the throwing off of imagos with more or less regularity, are below the average size of the species. These are to be regarded as juvenile communities which do not produce imagos because their numbers are not strong enough to feed to maturity individuals capable of maintaining an independent existence for a considerable period, and being, at the same time, capable of nourishing to an adult condition their immediate progeny upon the food-reserve acquired during their own development.

Nanism is seen at its highest expression in the first-born of a pair of termites. These reduced forms are so many abridgements of those of the community from which their parents sprang. They arrive at an adult condition upon a peculiar and limited diet, purely salivary, and this results in the dwarfing of the creature as a whole and in the reduction of the number of joints of its antennæ. From the study of both incipient and juvenile communities it becomes very apparent that nutrition has a considerable influence upon size and upon antennal developments. In a wide sense nutrition may be said to account for major and minor castes and for intergrading forms.

Of juvenile communities, those which are the most frequently observed belong to the genus *Eutermes*; locally, to the sub-genus *Trinervitermes*. Unfortunately for the classification of termites many *Eutermes* construct mounds early in their history—mounds easily explored by the itinerant collector. This, taken together with the failure of taxonomists to recognise nanism and its effect upon the antennæ, has led to the erection of a number of pseudo-species in this group.

From the evidence I have been able to gather, communities of fungus-growers are large and populous before a mound is built up above the nest-site. That they are dwarfs early in their history may be gathered from the smallness of the first offspring of mated couples. The disparity between such offspring of *Odontotermes badius* and the members of a

mature community is quite remarkable both as regards size and antennæ. From eighty pairs of imagos of this species, placed in artificial cells in February of 1917, two couples were maintained, one for fourteen, the other for seventeen months. Throughout the first winter the pairs remained in their cells making no effort to escape through the superimposed soil. It was not until spring that eggs were laid, and by midsummer each couple had a small brood about them. The young took approximately three months to arrive at the adult condition, and at the beginning of the fourteenth month the two colonies appeared to be well on the way to becoming established. The small workers went foraging, tunnelling through the surrounding soil and making their way to the surface, where they attacked vegetable particles placed there for them. In April one lot languished and the parents died; two months later (July 10th, 1918) a like fate overtook the second. The dwindling of the communities and the death of the parents were subsequently traced to predatory Acarinæ, doubtlessly introduced with the food placed for the convenience of the working parties.

The soldiers of these two incipient colonies were few and of one grade; the workers, although very small, were in two grades, and could be recognised macroscopically as majors and minors. In the accompanying table certain of the measurements and antennal details of the survivors are set out under A, and against them for comparison, under B, measurements taken from members of a large community found near where the winged forms were captured.

	A.	B.
Soldier:		
Antennæ XIV		XVII
Head width, 1·02-1·14 mm.		2·25-3·12 mm.
Mandibles, 0·8-0·89 mm.		1·37-1·69 mm.
Worker major:		
Antennæ XV, XVI		XVII, XVIII, XIX.
Head width, 1·08-1·14 mm.		1·5-1·8 mm.
Worker minor:		
Antennæ XIV		XVII.
Head width, 0·8-0·91 mm.		1·10-1·30 mm.

Respecting the antennal expressions it may be added that of A, those of XIV and XV are arrested or abridged forms of XVI, whilst the XVII and XVIII of B are similar forms of XIX; therefore there existed a considerable difference in the degree of development.

MATERIAL.—My earlier collections were made with the main object of ascertaining which of our species were most concerned in the destruction of cultivated plants and buildings. Consequently they were largely composed of many workers and a few soldiers. More recently one of the chief objects was to secure imagos and imago-nymphs in various stages of development, and these latter collections are, incidentally, fairly representative of the post-embryonic phases of the several castes. The material was mainly preserved in alcohol, and the technique employed was of the simplest.

It was early found that in order to ascertain the variation in the number of joints of the antenna of a given caste, it is very necessary to examine a lengthy series before any positive conclusion is arrived at or the antennal index decided upon.

TERMS.—There is, I think, only one term for which I need make any apology, and it is the word "larva." This is applied to the undifferentiated forms in the earlier stages of development, and, however at variance with good practice, the use of the term is very convenient and leads to less prolixity. The word "nymph" is employed more or less as a comparison to the word "callow." Thus "nymphs" are those forms which, by the possession of wing-sacs, may be regarded as the precursors of winged adults, and "callows" are soldiers and workers in the penultimate stage for which a distinctive term is desirable. For brevity the word "imago" is used in referring to winged males and females—the only reproductive forms coming under notice. Once they have completed their development, soldiers and workers are spoken of as being "adult," in the sense that they are "grown up."

2. THE LIFE-HISTORY OF A TERMITE.

The main outline of the life-cycle is now given, as the

development of the termite antenna is naturally correlated with it. Unfortunately it is practically if not wholly impossible to follow from day to day the growth and external metamorphoses of the same insect, and one can only draw a series of inferences from the condition of many in successive stages of development. With the multiplicity of forms to be found in a typical termite community, coupled with considerable difference in size of an individual at the beginning and the ending of a stadium, it will be understood that it is by no manner of means an easy matter to distinguish amongst them. Moreover, although attempts have been made to obtain complete series of certain species, no matter how careful one may be there always appear to be blanks. Consequently, I can but offer a hypothetical case which must not be taken too literally, and which, whilst it seems to fit the development of the antennæ and to account for certain divergences, calls for much deeper inquiry than I have yet given to it.

In the accompanying table (fig. 1) the transformations of the imago are set out in the left-hand column, and those of the soldiers and workers in the right. Including the egg, there appear to be seven stages for the imago and six for the two other castes. Inasmuch as the soldiers and workers of my incipient colonies took two to three months to reach the adult condition, this is probably the period under ordinary circumstances. Although these were abridged forms and may have been hastened to the adult condition, yet in a large community where food supplies are ample it is probable that the period would be no longer; it might even be less. The time taken by imagos to develop is known to be an extended one; with certain smaller-bodied species it seems to be one of six months, whilst with our fungus-growers and with *Rhinotermes putorius* the data collected point to it being about nine months. Upon this alone it is not unreasonable to assume an additional instar for the imago, more especially as it is a store-house of reproductive elements and of nutritive matter. However, the ascribing of the extra stadium of

TEXT-FIG. 1.

WINGED IMAGO.			SOLDIER AND WORKER.		
Stage.	Condition.	Instar.	Stage.	Condition.	Instar.
1	Egg.		1	Egg.	
2	Undifferentiated larva.	I	2	First undifferentiated larva.	I
First Quiescent period of Ecdysis.					
3	First imago nymph.	II	3	Second undifferentiated larva.	II
Second Quiescent period of Ecdysis.					
4	Second imago nymph.	III	4	Third undifferentiated larva.	III
Third Quiescent period of Ecdysis.					
5	Third imago nymph.	IV	5	Callow soldier and worker.	IV
Fourth Quiescent period of Ecdysis.					
6	Fourth imago nymph.	V	6	Adult soldier and worker.	V
Fifth Quiescent period of Ecdysis.					
7	Winged imago.	VI			

Illustrating the metamorphoses of termites, showing seven stages in the life-cycle of the reproductive winged form and six stages in that of the soldier and worker.

growth and ecdysis rests mainly upon the development of the spiracles and to but a very limited extent upon antennal conditions. The spiracles of the imago, those of the female in particular, are more specialised than are those of the soldiers and workers; as such they require an extra moult to come to the stage they are in. When in the fifth instar there is a certain amount of agreement between the spiracles—that is, between those of the imago nymph and of adult soldiers and workers; and, as these organs do become more specialised with ecdysis, as shown in a previous paper, I see no other explanation. The antennæ of the imago termites are on the whole more uniform than are those of the other castes; if we find the final number of joints is XIX, the nymph of the fifth instar has also XIX. This shows that the organ acquires its full complement of joints in the fourth stadium or with the penultimate ecdysis. Ordinarily the antennæ of soldiers and workers acquire their full complement with the third ecdysis or before that, but there are cases which can only be explained on the basis of a certain amount of joint multiplication taking place in the fourth instar.

Individuals which will become imagos commonly develop wing-sacs in the second instar and these increase noticeably with each ecdysis.

It has been established by Snyder¹ for certain North American termites that, when the transformation from the undifferentiated form to the soldier takes place, the individual becomes quiescent. I have found each ecdysis to be accomplished during a distinct resting stage, in which the insect assumes a very pupa-like attitude. This has been ascertained for so many species that I feel justified in accepting it as common to all. The period of quiescence is by no means transient and extends over several days. The process of moulting is accompanied by suppressed movements. The exo-skeleton is ruptured dorsally and pushed away by the spines when these are freed from it. It falls away towards

¹ Snyder, Thomas E., 'Science,' October 3rd, 1913.

the front, whilst with imagos the wing-sacs are withdrawn slowly from their sheaths. With all castes, however, the exuvia is delayed at the head; here it lies for some time in wrinkled folds around the bases of the antennæ, and until these organs are withdrawn or the cuticle breaks away the mouth-parts are masked. Even the legs are freed before the head. As a rule the exuvia appears torn away from the anal extremity and individuals are long active before the intima of the proctodæum is disengaged.

The second column of the table (fig. 1), representing the phases in the life-history of soldiers and workers, is based generally upon serial examinations of the species *T. natalensis*, *T. waterbergi*, *O. badius* and *O. latericius*, and in the main upon the first and last mentioned.

Apart from the subtle problem as to whether the caste is predetermined in the egg, it is even very difficult to state exactly when the distinguishing characters of soldiers and workers first become discernible. In certain species examined it would appear that slight differences can be detected in the third instar. The transformation to a soldier takes place during the third period of quiescency, so that after ecdysis the differentiation is most decided. A difference between majors and minors of the same caste is observable at the beginning of the fourth instar. The smaller grow but very little and become adult minors. The larger increase to twice their length and several times their bulk and become adult majors.¹ Here it is interesting to note that with those soldiers exhibiting a fleshy extension of the labrum, this part is visible as an internal metamorphosis of the third ecdysis and becomes disclosed with the final moult. The serrate nature of the soldier mandible of *Psammotermes allocerus* is also only disclosed with the last moult.

From among the quiescents of the third ecdysis in the

¹ According to Kellogg ('American Insects,' p. 105) Heath (1902) gives the soldiers of *Termopsis angusticollis* six moults, three of which are said to take place after differentiation. I have found no evidence of so many moults in the species I have examined.

O. latericius series I have been able to sort out the soldiers on the basis of the internal metamorphosis of the mandibles. These organs practically assume their adult character on entering the fourth instar; the heads of callow soldiers generally partake, however, of the worker type and may be wider than long. With *O. latericius* the change in the shape of the head from a subcircular to an elongate-oval outline takes place during the last ecdysis. Further, in the progress of the fourth instar the mandibles of all its castes become more and more deeply chitinised and coloured. This chitinisation starts at the tip and extends gradually to the base, the heaviest deposit being, with workers, along the cutting margin. In the last ecdysis of soldiers and workers, chitinisation, as manifest by pigmentation, has its principal seat in the head, the capsule and antennæ becoming pigmented. In the case of certain species a considerable degree of pigmentation of the antennæ of imago nymphs takes place in the fourth instar. The two main growing periods of the imago nymph are the fourth and fifth instars.

3. THE TERMITE ANTENNA.

(1) COMPOSITION.

All termite antennæ are composed of two sections—a scape and a flagellum. The scape is two-jointed, the number of joints in the flagellum is variable, ranging from nine to thirty and more. This subdivision of the organ is fundamental. With a few exceptions the two joints of the scape are robust and cylindrical—a shape they retain throughout development. The flagellum, often composed of joints of different shapes and sizes, may exhibit both specific and caste differences, and such distinctions may be radical or confined to differences in number or size of the segments. There is little variety of outline to be met with and few, indeed, depart from the moniliform type. Perhaps the most unusual is that exhibited by the soldiers of *Psammotermes allocerus*.

In many antennæ the conventional joint III is longer than

any beyond it and may be even longer than II. In some, III is particularly long and somewhat clavate, when it fore-shadows the third segment of the three-jointed scape of the specialised insect-antenna. In this striking form it is exhibited by the soldiers of *Calotermes durbanensis*. The antennæ of the imagos of this species occasionally exhibit III in the long clavate condition and it appears common to the imago antennæ of *Rhinotermes putorius*. Subsequently it will be shown that III of the adult organ is the repository of joint elements, and is in the wide sense a compound joint, variable as regards the joint elements it contains, because it represents the variable arrest of the formative zone.

By the suppression of an articulation one joint of the flagellum becomes ankylosed to another. Sometimes such ankyloses are aberrant and occasional, but on the other hand unions resulting from the fusing of sister elements may occur with sufficient regularity to become either specific or subspecific. The extent to which an articulation is suppressed, even when union occurs with characteristic regularity, is in some cases very variable, and ranges from a simple ankylosis, in which both segments retain their individuality, through all stages of combination to complete fusion. All these phases of union may occur in the antennæ of the individuals of one caste.

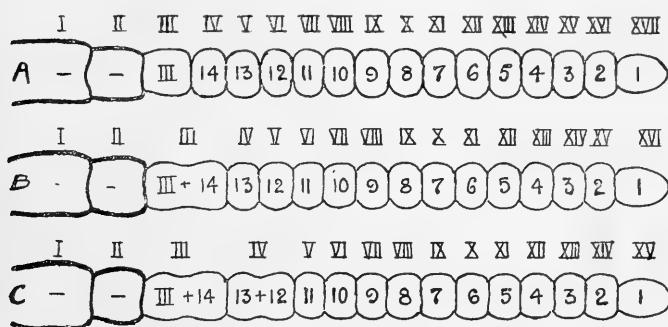
(2) THE NOTATION OF JOINTS.

In describing the composition of an antenna and the development of joints the conventional numbering of each segment from base to apex has grave disadvantages. It is, however, an established method and one impossible to discard. Further, the giving of the total number of joints for variable antennæ as an unqualified criterion is open to objection because it so often conveys a false impression of the nature of the organs. To number the joints in the sequence of their origin would be a very irksome matter, as those of the scape would be I and II, the apical III, the penultimate IV, and so on back to the scape.

As an instance of the varying totals leading to misconception those of a certain *Eutermes* may be brought under notice. The imagos are stated to have XV-, XVI- and XVII-jointed organs, and this conveys the impression of three quite different antennæ being developed in the same caste of the same species. Fundamentally all three are alike, being composed of the same number of elements with the number of joints reduced by the suppression of one or two articulations.

To meet such difficulties two systems of notation have been adopted. One is distinguished by Roman numerals, the other

TEXT-FIG. 2.



Diagrams illustrating the two methods employed for the notation of joints of the termite antenna. The conventional, in Roman numerals, shows A to be of XVII, B of XVI, and C of XV joints. The unconventional method shows all three to have a like composition.

by ordinary numerals. The Roman numerals are employed for any conventional statement or count, the ordinary numbers to indicate the elemental nature of the flagellum as from its apex to its base. This method is employed in fig. 2 for the three variations of the *Eutermes* cited above, and it will be seen that, notwithstanding the different counts, the elemental condition is the same.

(3) THE PROCESS OF JOINT-MULTIPLICATION.

The process of joint-multiplication is an internal metamorphosis accompanied by an external; and, as in the case

of certain other organs, the internal is in advance of the external. In other words, in a developing termite the appropriate jointing of the antenna for one or more succeeding stadiums becomes clearly marked out in the soft tissues long before an inner new layer of chitin is produced preparatory to ecdysis. The external may first be discussed, and the internal described in a later section dealing with the subdivision of joint III.

The new joints are at first indicated externally by annulations. They then abjunct in a somewhat rudimentary form, and, as they become larger and more decidedly articulated, slowly develop in character, whilst a whorl of long setæ gradually grows from them; later they become more haired, and, in some cases, a second whorl of long setæ grows. It would appear that, once abjuncted, although a joint may become quite attenuate, it never again sub-divides.

In the abstract the process is simple, and may be said to represent the insertion of new joints between III and IV, or the formation of joints at the expense of III as stated by Müller and Sjöstedt. Where this takes place the joints are ordinarily added two by two, the distal being always larger and in a more advanced condition than the proximal. In some antennæ the addition seems to be one by one, but this is only because the proximal member of a pair is more delayed in its development than is commonly the case. The process in the antennæ of *Hodotermes* is not readily followed; it is somewhat exceptional, and is to be considered as omitted from this general statement.

(4) JOINT III AND ITS SUBDIVISION.

Joint III is a link between the flagellum and the scape, a receptacle for joint elements, a womb wherein they undergo a certain amount of development before being abjuncted as rudimentary joints. Except in the antennæ of *Hodotermes*, and possibly other species with multi-jointed organs which I have not examined, joint III elongates and subdivides

repeatedly. In the case of *Hodotermes* the joint certainly has an analogous nature, but the addition of new joints is not due to an obvious subdivision of the whole—indeed, the rudimentary joints have rather the appearance of being budded at the apex of II.

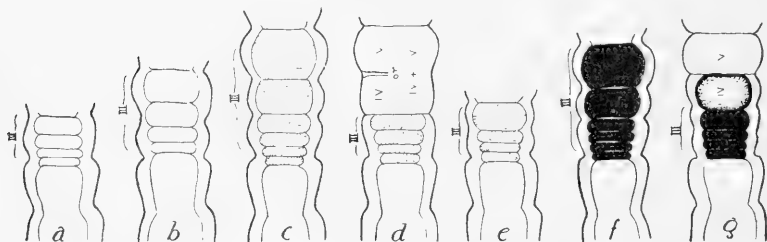
Doubtless the mode of joint formation in III seen in most species is a modification of the more generalised condition of *Hodotermes*, arising from the slowing down of the process and the production of fewer joints. To explain adequately the difference in the mode of joint formation in *Hodotermes* and in the remaining termites, a detailed embryological investigation is essential.

The cycle of external changes recurring in III is more readily recognised in the antennæ of some species than in those of others. In some there is no difficulty encountered in deciding, upon exterior features alone, what phase the part is in; in others one may be readily deceived. In the former the subdivision results in the more or less coincident abjunction of two joints of nearly equal development (fig. 3, *a-d*). In the latter there is a decided difference in the degree of development of the two joints, and the premature incipient abjunction of the predominant partner gives the impression that the joints arise one by one and leads to one abjuncting joint being regarded as belonging to the formative zone (fig. 3, *e-g*). This difference, at the beginning of my study, led me to premise two modes of joint-multiplication—the production of joints as pairs and as single individuals. An examination of the internal metamorphosis shows, however, that the difference is but one of degree. Both modes are illustrated in the accompanying series of diagrams. Fig. 3, *a-d*, show the internal and external changes noted for the one, and *e-g* for the other. A comparison of these two modes indicates that on the coincident abjunction of two joints III becomes monolocular in the one (*d*) and bilocular in the other (*g*).

The first mode may be used to describe the development of all antennæ and to explain the origin of the various patterns

met with, as it is the less involved and the results are the same. It may be described briefly as follows: In the monolocular form (*a*) III contains four elements in a more or less compressed condition. These represent two pairs, and of each pair the proximal element is the smaller. With the growth of the distal pair III becomes bilocular (*b*), and from this it passes through a faintly to a distinctly trilocular state (*c*), when two new elements arise. Subsequently the two outer loculi abjunct as rudimentary joints (*d*) and III reverts to its monolocular form as the receptacle of four elements, two of which are new. Speaking generally, the

TEXT-FIG. 3.



Diagrams illustrating the external and internal metamorphoses of joint III and the abjuncting of rudimentary joints.

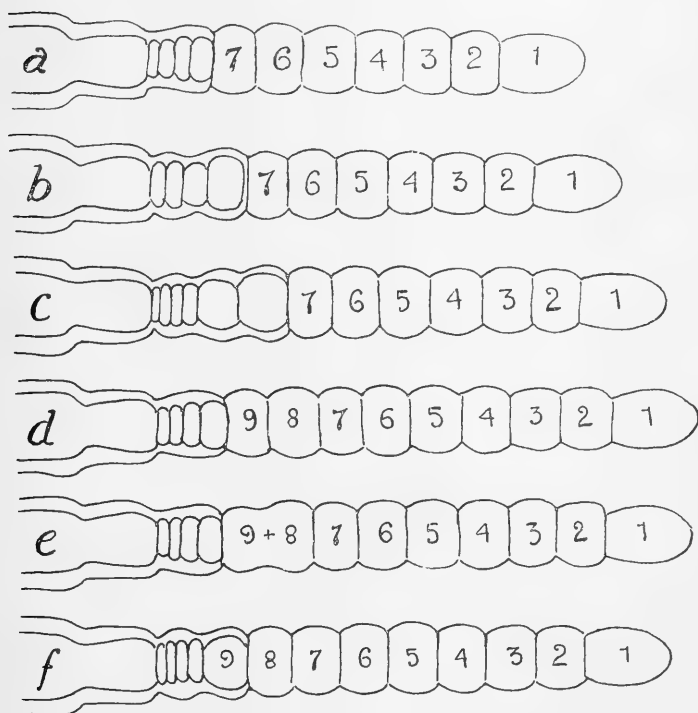
number of abjuncted joints in the flagellum of the newly hatched termite is either seven or nine. Hence the last abjuncted joint in a developing organ is the odd number of a pair, e. g. 9, 11, 13, 15, etc., the pairs being (8-9), (10-11), (12-13), (14-15), etc. This fact may be made use of in determining the condition of antennæ developing by the second mode; if what appears to be the last joint abjuncted has an even number, when counted from the apex towards the scape, it is because its companion has not been distinctly segmented off from the stem.

With both modes there is a decided tendency for the articulation, or line of fission, dividing paired or sister elements to become suppressed. This results in the abjuncting of a compound joint, and if the articulation is quite

suppressed, the joint may be simple in outline ; otherwise it will be more or less bilocular.

When the process is subsiding there is a marked tendency in the first mode to change to the second, and thus it frequently happens that antennæ will be finally odd-jointed

TEXT-FIG. 4.



Diagrams illustrating antennal development and joint multiplication.

although originally progressing to an even total. This is due to the fusing of the joint-elements and the disappearance of the lines of fission, i. e. the series of elements is transformed into a homogeneous column.

There may, therefore, be two forms of compound joints in the flagellum—those which result from the fusing of sister elements and giving rise to compound joints removed more

or less from III, and the compound which III itself represents.

The several points in the foregoing discussion may be illustrated hypothetically by fig. 4, *a-f*. Diagram *a* represents a X-jointed expression with III monolocular; in *b* the bilocular and in *c* the trilocular conditions are given. Ordinarily the increase in the number of joints is as represented in *d*, in which the two new joints are (8) and (9) and the X expression has definitely become a XII expression. Should the articulation between (8) and (9) be suppressed and the two abjoined as a compound joint the X will become an XI expression as in *e*. Should the process subside more or less suddenly, whilst in the stage of *c*, a long III will form about the six elements then present, and the organ will remain X-jointed. If the subsidence is more gradual, one joint (8) will abjoin, as in *f*, and give rise to an XI-jointed organ of which III encases five elements.

(5) EMBRYONIC DEVELOPMENT.

The development of the antenna has two stages, the embryonic and the post-embryonic. The degree of development when the egg hatches appears to differ in different species. Thus the young of *Cryptotermes* shortly after birth have organs specifically X-jointed, but which may appear VIII- or IX-jointed. The antennæ of most species are, at hatching, X-jointed with the elements of XIII; others again are XII with the elements of XV. Joint III thus contains four joint-elements in the form of two sister pairs.

The embryo at maturation possesses organs having the appearance of elongate sacs attached to the two-jointed scape. Within these sacs a series of septa may be seen of which those towards the apex are the more distinct. The impression one gathers is that the scape develops first and the flagellum is produced therefrom; but a definite study of the embryology is much to be desired.

(6) JOINT MODIFICATION.

Any decided modification of the joints of the antennæ is coincident with an ecdysis and preceded by the subsidence of the process of multiplication. Upon the whole the shape of the joints in imago antennæ alters only with the last ecdysis, and is mainly restricted to the lengthening out of certain joints in the flagellum. There are also slight changes of form following chitinisation. The antennæ of workers are modified but very little; they become pigmented in the last ecdysis and more chitinised after the adult stage is reached.

With soldiers as a rule multiplication subsides before or during the penultimate ecdysis, and in some species the organ as a whole is so considerably modified during this period of quiescency that after the moult some of the joints have shapes very different from those of the third instar. As a rule the more the shape of the head departs from the larval type the more the antennæ are modified. Later, with chitinisation further changes may be accomplished, such as the obliteration of evidence of imperfect articulation.

Two of the most striking cases are those occurring with the nasuti of the *Eutermes* group and the soldiers of *Psammotermes allocerus*. With the nasuti, the remarkable cephalic prolongation called the nasum develops during the penultimate period of quiescency, and at the same time certain of the joints lengthen out in proportion with the cephalic projection. Consequently the callow of the fourth instar exhibits a head and a pair of antennæ differing very little from those of the final form. In the case of the soldiers of *Psammotermes allocerus*, after the penultimate ecdysis the antennæ present an extraordinary change of appearance. The basal series of joints in the flagellum becomes swollen at the base—a reverse of the shape of the undifferentiated and adult stages. Notwithstanding this disparity, they foreshadow the form of the adult organ, and, later in the instar, the swelling at the base of the joints is transferred to the apex so that they become more or less clavate.

(7) ASYMMETRICAL ANTENNÆ.

The antennæ of the two sides are quite commonly asymmetrical in minor features which do not call for special comment. Not infrequently with certain species a difference occurs which does not extend beyond the degree to which a given articulation is suppressed in one and not in another. In one organ the suppression is complete, and leads to a compound joint of simple appearance, whilst in the companion organ the joint may be bilocular with or without a pseudo-articulation, or the articulation may be normal. Although such differences indicate an asymmetrical development it does not necessarily result from any deep-seated influence.

With certain soldiers the difference between pairs is fundamental, one organ being of more joints than its companion, because it has grown for a longer period. Marked as such differences are, they do not extend to other external parts. It occurs to me that these marked cases may be traced to an asymmetrical atrophy of the reproductive organs, just as the difference in size as between majors and minors may be traced to the quicker or slower degeneracy thereof.

(8) POLYMORPHISM.

There may be said to be two orthodox views regarding polymorphism among termites. The one is that the caste is predetermined in ovo, and we understand this phenomenon as little or as much as we are content to understand the predetermined difference between male and female. The other view is that the infertile soldiers and workers have their cause in the quality and quantity of food supplied to the developing individuals. This theory arises because it has come to be regarded as actually true that all termites feed their young. It premises all the larvæ as potential males or females; but from the many only a few become sexually mature because the majority are so treated that they undergo an abridged development, and of those undergoing

this, some—the soldiers—by extended treatment become highly specialised.

If the second view is to hold good it follows that with those species exhibiting four well-defined infertile castes there is a very accurate determination of the food-supply to produce majors and minors accompanied by peculiar differential feeding, amounting to doctoring, to produce soldiers from some of these.

I find it quite impossible to regard the infertile members of such a community as dependent upon a post-natal treatment, since they could only result from an incomprehensible and complex treatment practised upon a multitude of individuals daily augmenting an already populous community.

The fungus-growing *Termes natalensis* has four sharply defined infertile castes. The workers carry the eggs from the queen cell and stack them in the fungus garden. Here they hatch, and with them are to be found, inextricably mixed, thousands of developing forms representative of all castes and stages, and only accompanied by about one adult worker to the thousand. Apparently undifferentiated at birth, the young are surrounded by a particular kind of food, and their mouthparts are sufficiently well-developed to tear off portions of the delicate tissue composing the well-known white spheres. If it be argued that they do not subsist upon this substance the following questions present themselves:

(1) Why are they, as eggs, brought to such places as those where the spheres are most abundant?

(2) Why cannot one see and record overwhelming evidence of the young being fed by the workers?

(3) Why are the immature forms present in the fungus garden in all stages of development, whatever their ultimate form?

As it can be readily demonstrated that the immature forms feed regularly upon the cells which compose the white spheres, how can their different traits be attributed to the withholding or giving of food when the opportunity for all must be alike?

This leads me to suggest that further light might be thrown upon the subject of polymorphism by inquiring into the origin of fertile forms of a community of fungus growers.

It is conceivable that conditions within the nest have become so peculiar and artificial, as it were, that it is the fertile caste which requires special food in order to develop, and that under the ordinary conditions obtaining in the nest the abridged development is the normal course. The individuals ultimately becoming winged males and females assume an imago character after the first ecdysis, as then the vestiges of wings arise. Possibly these forms have received some special treatment in the course of the first instar. Early they develop distinct characters by which they can be recognised, e.g. wing-sacs. They certainly have a greater opportunity for taking food because their pre-adult existence is prolonged, and it may be accepted that they receive special and generous nutrition, even if there is no direct evidence on this point.

Should the winged forms arise in a manner of this sort it is not extremely difficult to account for pteroergates, for the vestiges of wings these possess and for their occasional additional features. Pteroergates may then be regarded as forms partly treated or ineffectively treated.

Unabridged development cannot be caused by a seasonal influence, as, if it were, the community would be generally affected and the winged forms would come to maturity in a very regular manner. But this is not so. Individuals that will become males or females begin to appear some time after the last of the previous brood of winged imagos has left the nest, and the ultimate number produced in a season is due to a gradual augmentation over several months. Indeed, at certain times with many species imago nymphs are in great variety as regards the degree of their development, and later, when some are winged and quite mature, others are far from full development. Undoubtedly any general exodus of winged individuals is delayed until a propitious moment, and when that moment arrives the majority are capable of participating in it.

PART II: SYSTEMATIC REVIEW.

1. INTRODUCTION.

IN this part an attempt is made to set out concisely an account of the antennæ I have examined. The variations met with are discussed and the different compositions found in each species are homologised. Ordinarily, under a separate heading, some account of the development of the organs is given, and each is based as far as practicable upon serial examinations of the organs of the developing forms. Unfortunately, however, the material for certain stages was very limited in some cases, and often, where a great many antennæ were studied, the result in the aggregate was no great compensation for the task.

It was my intention, at the outset, to supplement each discussion with a complete series of drawings. This, however, would have resulted in a multiplicity of many figures bearing so much likeness to one another that they could only lead to confusion. The homologies of the antennæ have, therefore, been illustrated by outline figures prepared from camera lucida drawings. When conveniently possible the various antennæ of a species are drawn in proportion.

Illustrations of the developing organs in the different species have been practically eliminated, as it was found possible to arrange all cases in a composite chart. This is given as Plate XV. The chart comprises thirty-seven diagrams and represents the phases of development which come under reference. For the sake of convenience and conciseness these phases are referred to in discussing a given development as "stages," and in both chart and in the discussions these are treated very much as one does a genealogical statement. The main route of development for a hypothetical XX or pseudo-XXII-jointed organ is traced through its various phases from a X, pseudo-XII-jointed, condition in the sixteen diagrams **A** to **P**, the increase being represented by the insertion of the five pairs of joints (8-9),

(10-11), (12-13), (14-15), (16-17). In the series the cycle of external and internal metamorphoses of joint III is recorded and the difference between a joint in posse and a joint in esse is illustrated by the notation. Thus the difference between diagram **A** and diagram **B** is that the sister-joints (8-9) are numbered in **B** because they have abjoined and are to be regarded as separate entities, whereas in **A** they are the two distal loculi of joint III. This also explains the difference between a pseudo-XII-jointed and a definitely XII-jointed expression.

Hypothetically, an organ may be arrested in any one of the phases or stages **A** to **P**. Very frequently, however, they are arrested in a transition from one stage to the next. Thus **P** represents a pseudo-XXII-jointed organ, and this becomes XXI when only the distal loculus abjoins. This arrest in transition is illustrated by diagram **Pb**, and represents those cases where an organ progressing to an even total of joints becomes odd-jointed. Thus **Nb** is a XIX-jointed organ derived from a pseudo-XX, **Kb** a XVII from a pseudo-XVIII, and **Db** a XV from a pseudo-XVI.

Other variations are due to the abjunction of the two loculi of III as a compound joint; thus diagram **AB** shows an XI-jointed expression derived from the pseudo-XII of **A** as the result of the union of the first pair of sister-joints (8-9); **DE** shows the abjunction of the second pair of sister-joints as a compound (10-11); it is described as **DE** because it is derived from **D** and is elementally homologous with **E**. The same applies to **GH**, **JK** and **MN**. The development of antennæ may or may not continue after such a compound has abjoined. The most extraordinary cases of this occur in the antennæ of *Termes waterbergi*, especially those of the imago. These are not charted. The more common developments taking place after the fusing of two joint elements to form a compound joint are illustrated by the series **GH** to **GL** and **JK** to **JO**.

A comparison of **Kb**, **K**, **JK**, **GK** and **GKb** shows five forms of antennæ all differently composed yet elementally homologous.

The potential development of an antenna to the third ecdysis seems to be twenty-three joints. That is, it may arrive at the stage **M**, which is pseudo-XX-jointed. At this stage III contains six elements, there are fifteen abjoined joints and the two-jointed scape. The two species, *T. bellicosus* and *T. natalensis*, may be cited in this connection. The antennæ of these ab ovo are in stage **C**, which is a potentially fifteen-jointed ($I + II + 0 + 0 + 0 + 0 + 9$ to 1). Their development therefore represents an increment of eight, and the same is the case with those species such as *Odontotermes latericius*, of which the ab ovo expression is the pseudo-XII of stage **A**.

This leads me to surmise that the elimination of joint multiplication with or soon after the third ecdysis was the most important step in the reduction of the antenna. With imagos the arrest coincides with the beginning of a period of special nutrition, a preparation stage for a long fast, a fast including the tending and feeding of young. The curtailment of development is therefore directly traceable to the social habit, the multi-jointed organ of the non-social ancestor being sacrificed to a new necessity.

2. STUDIES OF SPECIES.

(1) *Hodotermes viator* (*Latreille*). Fig. 5, *a-g*.

ANTENNAL INDEX.—Imago XXVII, XXVI; soldier XXVII, XXVI, XXV, XXIV; worker XXX to XXV.

In all castes and in all species of the genus *Hodotermes* the antennæ are very much alike, irrespective of the number of joints of which they are composed. This is mainly traceable to the curtailment of joint-multiplication and the subsidence thereof not being accompanied, to any noticeable extent, by the formation of compound joints. It is also partly due to the simple annular nature of the majority of the segments. Compound joints are not entirely absent, but when present are located in the more juvenile section of the flagellum and are never conspicuous.

There are two points of difference between the antennæ of *H. viator* and those of any other species at present coming under reference. In the first place the minimum number of joints for all castes is twenty-four, whereas in other species the maximum is twenty-one. In the second place *H. viator* imagos exhibit fewer joints than do their largest workers; in species of other genera workers or soldiers may have as many joints as the imagos, but never more and frequently less.

All the imagos I have examined from south-west Cape to as far north as the Orange River agree in having XXVII- or XXVI-jointed antennæ, and a XXVI is always due to the presence of one compound joint near to the base of the flagellum. The number XXVII therefore approaches a specific character; it appears due to the subsidence of joint-multiplication during the fourth instar and before a possible fuller expression has been reached.

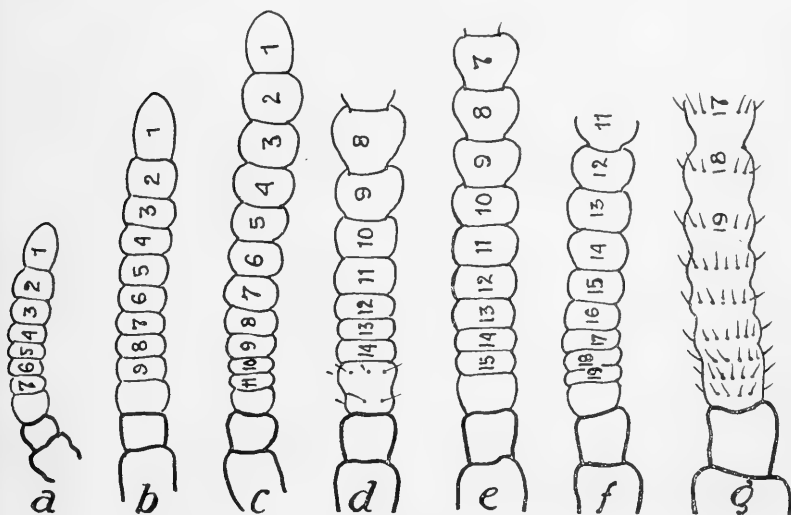
The antennæ of workers range from XXV to XXX in an unbroken series, and the rule is, the larger the individual the greater is the number of joints. As the largest workers have more joints in their antennæ than do the imagos it is assumed that in the former caste the larger insects lean more towards the primitive condition.

As the differences in the antennæ of workers and of soldiers are only differences in the joint totals, it is supposed that they are due to more or less joint-multiplication taking place in the fourth instar. If joint-multiplication ceases at the beginning of the instar there are twenty-five joints; if later there are more. However, the XXX expression for the largest workers cannot be regarded as a possible maximum, but rather as a specialised limitation, because in the larger and more generalised species of the genus the largest workers may possess organs of as many as thirty-five joints. In the soldier antennæ the totals range from XXIV to XXVII, and here, as with the workers, size and number go together. The lower minimum and maximum are probably traceable to cephalisation.

DEVELOPMENT.—Unfortunately it has not been possible to

trace the development of the *Hodotermes* antennæ satisfactorily. The embryo, just before hatching, and the smallest larvæ have antennæ (fig. 5, *a*) which may be regarded as being in stage **A** (Pl. XV), the transition of a X to a XII expression. These develop to a definite XII-jointed organ (fig. 5, *b*), in which III divides and exhibits an internal metamorphosis (stage **B**). Subsequently two rudimentary

TEXT-FIG. 5.



Hodotermes viator (Latreille). *a. b.* Antenna in first instar.
c. Second instar, *d-f.* Third instar. *g.* Large worker fourth instar.

joints, (10) and (11), abjunct (*c*), and stage **E** is arrived at. This is probably the condition of the organ in the second instar. Later developments, which I take to be those of the third instar, are represented in fig. 5, *d-f*, the new joints numbering three, four and eight respectively. The organ illustrated by (*g*) is taken to be that of a larger worker of the fourth instar and seems to indicate the adding during this period of an indefinite number of joints.

(2) *Termes waterbergi* Fuller. Fig. 6, *a-t*.

ANTENNAL INDEX.—Imago XIX, XVIII (XX); major worker XIX; minor worker XVIII, XVII; major soldier XIX, XVIII, XVII; minor soldier XVII.

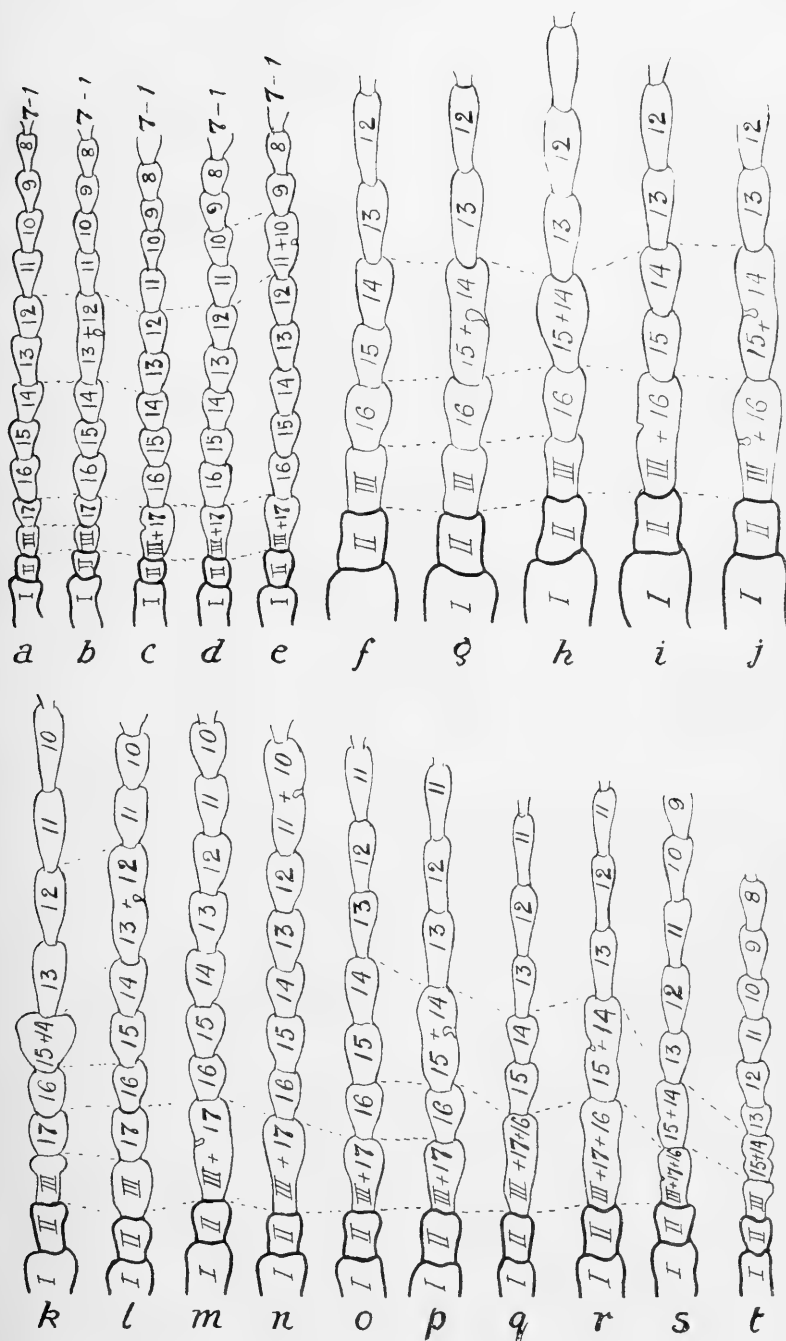
Although related to *T. bellicosus* and *T. natalensis* this species is more generalised, and its antennæ, especially those of the imago and major soldier, may be regarded as being transitory or unstable. A further study may show the homologies to be upon a slightly different basis, because perhaps certain joints herein treated as simple may have been evolved from the amalgamation of paired joint-elements. That simple joints now always simple may have been so evolved follows the general process of specialisation by reduction, and is not in antithesis with any deduction or explanation previously or subsequently given. To take the possibility fully into consideration here or in dealing with antennæ of other species would entail involved explanations and serve no useful present purpose.

The only castes of *T. waterbergi* in which I have found constant antennæ are the major worker and minor soldier; the organs of these, as indicated in the antennal index, are respectively XIX- and XVII-jointed.

IMAGO ANTENNÆ.—Although in pairs of antennæ the arrangement of the joints agrees, there exists a noticeable inconsistency as between the pairs of different individuals. This is quite unusual for the caste with species in general. However, the variations met with are all due either to capricious unions of sister-joints or to the more usual union of the conventional IV with III. As a rule these unions are readily recognised by the presence of fairly distinct pseudo-articulations or, when such are absent, by the elongate nature of the compound joint. Virtually the antennæ are all of XX segments, but count XIX or XVIII by the suppression of

TEXT-FIG. 6.—*Termes waterbergi* Fuller. Diagrams *a-e* illustrate antennæ of imagos, *f-j* of major soldiers, and *k-t* indicate the homologies for all castes.

TEXT-FIG. 6.



either one or of two articulations. The variations met with are represented by fig. 6, *b-e*, and these are homologised with an imaginary XX-jointed expression (*a*) derived from the condition of (*b*) and (*c*). The antenna (*b*) would be XX-jointed but for the capricious (13 + 12) combination, and the antennæ (*c*) and (*d*) would be equally so but for the (III + 17) union. The antenna (*e*) passes as one of XVIII joints, as it has two unions—(III + 17) and (11 + 10).

MAJOR WORKER ANTENNÆ.—The antennæ of the major worker are, on the other hand, remarkably regular both in the number of joints and in general pattern. I have always found them characterised by a peculiar buffer-shaped III and a very coarse VI, with a series of attenuate joints distal to VI; at least this was the case with those of over one hundred individuals examined.

One of the objects of this extended examination was to ascertain if a pseudo-articulation was ever present in III or in VI which would demonstrate their suspected compound condition. The search was unavailing, but resulted in finding five antennæ in which joint VII exhibited a pseudo-articulation. In examining developing antennæ, however, it was quite an easy matter to demonstrate III and VI to be compound, although no evidence was obtained to show VII the same. These few examples, in which VII appeared compound in the adult, may represent atavism and indicate that the joint was evolved from a union of two elements. If this is a correct inference it can be shown that VIII is also similarly evolved. Nevertheless, the joint is treated as simple in this discussion because it develops apparently as a simple joint. By accepting joints VI and III as compound the notation of the worker antenna is as in fig. 6, *k*, VI being accepted as a (15 + 14) union.

MAJOR SOLDIER ANTENNÆ.—Between the antennæ of the imago and major soldier there exists certain superficial resemblances. These latter organs can be homologised among themselves (fig. 6, *f-j*), but the unions are not those

common to the imago. Fig. 6, *f*, of the series represents the XIX expression of the major soldier. Both the XVIII (*g*, *h*) are derived from the XIX by a $(15 + 14)$ union, whilst the XVIII (*i*) is due to a $(III + 16)$ union. The XVII (*j*) is due to two unions, a $(15 + 14)$ accompanied by a $(III + 16)$.

THE HOMOLOGIES.—These are set out in fig. 6, *k-t*. All the figures employed are from camera-lucida sketches, but are not absolutely in proportion. With the exception of the antennæ of the minor workers (*t*), all represent the same degree of development—that is, the flagellum of each contains the same quota of joint-elements, namely twenty-one. In the flagellum of the minor worker there are, however, only 19 elements. The main point of difference between the antennæ of the major worker and imago is that in one there is a constant $(15 + 14)$ union which is always absent from the latter. The main points of agreement between the organs of the major worker and major soldier lie in the frequency of the $(15 + 14)$ union in the soldier organ and the peculiarly attenuate nature of (13) and (12) in both.

The XVII expression of the major soldier (fig. 6, *r*) is quite uncommon, but homologises with the constant XVII of the minor soldier (*s*), as a comparison of the two sketches shows. The antennæ of the minor workers, as represented by (*t*), show their curtailment by the absence of (16) and (17). In a few cases they must be regarded as XVIII-jointed as (14) and (15) are practically independent joints.

DEVELOPMENT.—The natal condition of the antenna is as represented by stage **C** (Pl. XV), in which III is in a bilocular phase. This seems common to all undifferentiated larvæ at the beginning of the first instar.

Imago.—The antennæ developing along the main route **C** to **M** become XIX-jointed by the abjunction of (16), leaving III composed of $(0000 + 17)$ as in stage **Nb**. This is the more common antenna; in it (16) the conventional IV is usually large and might be taken as a development to **MN**. Its true condition, however, is revealed by the internal arrangement of the elements of III when in the last nymphal instar.



Should the developing organ reach stage **N** it would be by a XX-jointed expression. This I believe it occasionally does, but such of those examined as would have been XX-jointed had been reduced to XIX by capricious fusings such as (11+10) which took place as in stage **DE** or of (13+12) as in stage **GH**. The total elements in the flagellum of all patterns may be regarded as 21.

Major Worker.—These antennæ develop from stage **C** to **J**; at this point (15+14) are abjoined as one joint (stage **JK**). The organ then passes through **JL**, **JM** and **JN** to **JO**. It, therefore, has a slightly greater development than the imago organ; but this is confined to III and leads to the peculiar buffer-shape of that joint. The number of elements of the flagellum is 21.

Minor Worker.—The development of these organs either follows the direct route **C** to **K** and they become XVIII-jointed, or diverges from **J** to **JK**, by the fusing of (15+14). In both cases the flagellum elements are not less than 19 and may be 21.

Major Soldier.—A few of the major soldier antennæ develop along the same route as do those of the minor and become XVII-jointed. Some following the **C**, **J**, **JK** route pass from **JM** to **JNb** and become XVIII by the abjunction of (16). Others follow the direct route **C** to **M**, when they remain XVIII-jointed due to the suppression of articulations developing in III, so that III comprises (0000 + 17 + 16), or they pass to the stage **Nb** and become XIX-jointed, III representing (0000 + 17). The flagellum in all soldier antennæ is therefore composed of 21 elements.

Minor Soldier.—The antennæ develop from **C** to **J** and from **J** through **JK** to **JM**, at which stage one joint, more or less compressed in appearance, forms a (0000 + 17 + 16) combination. Here, as in the imago and worker major antennæ, the total of flagellum elements is 21.

Reduced to a formula the various antennæ are composed as follows:

Imago:

XIX: I	II	III (0000)	IV (17)	V (16)	VI (15)	VII (14)	VIII (13	+ 12)	IX (11)	X (10)
XIX: I	II	III (0000	+ 17)	IV (16)	V (15)	VI (14)				
VIII: I	II	III (0000	+ 17)	IV (16)	V (15)	VI (14)	VII (13)	VIII (12)	IX (11	+ 10)

Major worker:

XIX: I	II	III (0000)	IV (17)	V (16)	VI (15	+ 14)	VII (13)
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Soldier:

XIX: I	II	III (0000	+ 17)	IV (16)	V (15)	VI (14)	VII (13)
VIII: I	II	III (0000	+ 17)	IV (16)	V (15	+ 14)	VI (13)
VIII: I	II	III (0000	+ 17	+ 16)	IV (15)	V (14)	VI (13)
XVII: I	II	III (0000	+ 17	+ 16)	IV (15	+ 14)	V (13)

(3) *Termes bellicosus Smeathman*, var. *mossambicus*
Hagen. Fig. 7, *a-h*.

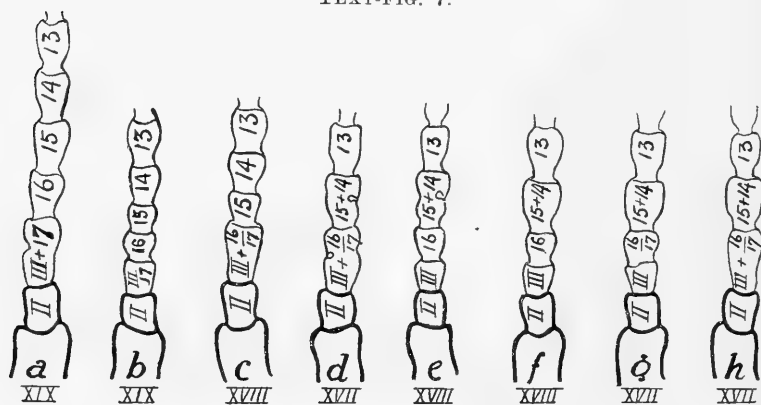
ANTENNAL INDEX.—Imago XIX (pseudo-XX); major worker XVIII; minor worker XVII; major soldier XIX, XVIII, XVII; minor soldier XVII.

The species under reference is placed as var. *mossambicus* as it is without doubt the one to which Hagen originally gave the status of a variety and to which his description, nowadays accepted as the standard for *T. bellicosus*, mainly applies. The material examined comprises collections made from nests on the banks of (i) the Zambesi, at Tete, the type locality; (ii) the Busi, about 30 miles west of Beira; (iii) the Limpopo, near Messina in the northern Transvaal; (iv) the Umkomati, at Xinavane in the district of Lourenço Marques; (v) the Umbulusi, near Delagoa Bay.

In all these collections except one the antennal index was found to agree with the descriptions of both *bellicosus* and *natalensis*, some of the imago antennæ being pseudo-XX jointed (fig. 7, *a*). From one nest, out of four examined at Xinavane, the major soldiers in more or less equal proportions exhibited organs of XVII, XVIII, and XIX joints. Fortunately the variations were such as to set at rest any doubt as to their homology. On reference to the figures it will be seen that all the deviations arise from fusions of the

conventional V with VI or III with IV of the XIX expression. The different forms are represented in fig. 7, *b-h*. The clue to the origin of the XVII-jointed organ (*h*) is given by (*d*); this counts XVII-joints, but both III and IV are decidedly compound and exhibit well-defined pseudo-articulations. In this expression III represents (III + IV) and IV represents (V + VI) of the XIX-jointed expression. In (*h*) the evidence of the fusion is lost. Other forms (*e* and *f*) are XVIII-jointed because only the conventional V and VI of

TEXT-FIG. 7.



Termes bellicosus Smeath. *a*. Imago. *b-h*. Soldier.

the XIX have fused; in one type (*e*) the compound nature of the joint is indicated by a notch and a decided pseudo-articulation, in the other (*f*) only by the length of the joint. The form (*g*) may be described as intermediate to an XVIII and a XVII expression. A few other minor variations also occurred in this series of antennæ, but all of a confirmatory nature.

DEVELOPMENT.—The development of these antennæ is parallel with that of those of *Termes natalensis* and all are treated as homologous with the XIX (pseudo-XX) imago organ, represented by fig. 7, *a*. To attain this expression the organ develops from stage **C** to **Nb** through **M** and is XIX-

instead of XX-jointed because (16) abjuncts as an orphan joint and leaves III composed of (0000 + 17). The XIX-jointed soldier expression (*b*) is regarded as a development through stage **M** to **Nb** parallel to that of the imago. Should no fission take place in III at the stage **M** the XVIII soldier expression (*c*) will result. The XVII expression (*h*) is a development through stage **J** to **JM**, and an XVIII expression may be derived through **J** and **JM** to **JNb** by the separation of (16) from III as in the form represented by (*f*).

(4) *Termes natalensis* Haviland. Fig. 8, *a-e*.

ANTENNAL INDEX.—Imago XIX (pseudo-XX); major worker XVIII, XVII; minor worker XVII; major soldier XVII; minor soldier XVII.

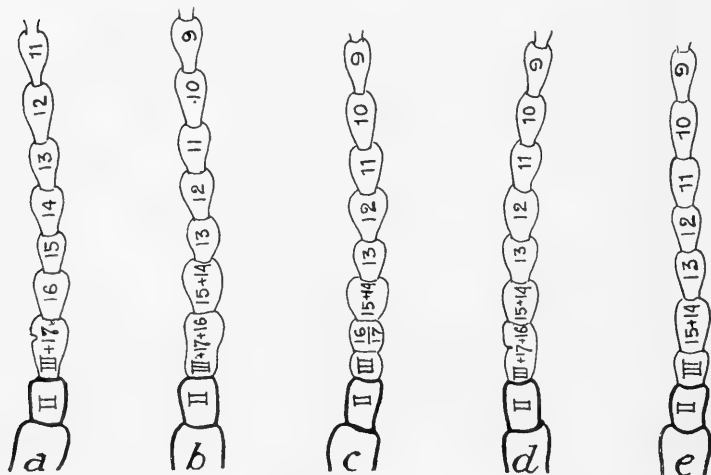
The antennal index is based upon the examination of so many nest series and so many antennæ that I have long since neglected to keep a record of them. Without doubt several topographical forms of *natalensis* are included in this review all of which are sufficiently distinct from *bellicosus*; two at least would be regarded, taxonomically, as individual species.

The imago antennæ are uniformly XIX-jointed except for some exhibiting a very decided notch in joint III, fig. 8, *a*, illustrating the evolution of this organ from one of XX joints. A precisely similar condition is also to be met with in the imago antennæ of *T. bellicosus*. The discovery of soldiers of the last-mentioned species with XIX organs, as detailed in the foregoing section, coupled with the agreement between the development of the antennæ of *T. natalensis* and *T. waterbergi*, is sufficient evidence for the homologising of all the soldier and worker antennæ of *T. natalensis* with those of the imago as in fig. 8, *a-e*.

DEVELOPMENT.—The antennal expression of the larva ab ovo is the same as in *T. waterbergi*, one of XII segments with III bilocular (stage **C**, Pl. XV). The development and changes of the formative III are also precisely the same.

Imago.—On entering the second instar the nymph of the imago exhibits a XIV expression (stage **E**), which, passing through stage **F**, becomes pseudo-XVI (stage **G**). In the third instar this passes to stage **J**, and during the third quiescent period the changes are such that it passes to the pseudo-XX, stage **M**, and after the ecdysis is XIX-jointed **Nb**, because (16) abjuncts as an orphan joint. Should (17) partly abjunct, III will show a notch, as it sometimes does.

TEXT-FIG. 8.



Termes natalensis Hav. a. Imago. b. Soldier. c, d. Major worker. e. Minor worker.

Soldier.—The antennæ of the major soldier, although always XVII-jointed, are such, in both the callow and final condition, that they are recognised as developments through stage **J** to **JM**, in which the composition of III is (0000 + 17 + 16) and of IV (15 + 14), providing one has become acquainted with the aberrant forms of *T. bellicosus* discussed in the preceding section. The organs of the minor soldiers are simply dwarfed replicas of those of the major.

Major Worker.—These organs, although sometimes counting one more joint than those of the soldiers, do not represent a greater development. The conventional V of the XVIII

or IV of the XVII expression is a (15 + 14) compound (fig. 8, c, d). This shows a development through **J** and **JK** to **JNb**, giving an XVIII-jointed organ in which III comprises (0000 + 17), or to **JM**, giving a XVII-jointed organ with III comprising (0000 + 17 + 16). The comparative shortness of III in the XVII organ is due to the arrested state of the elements.

Minor Worker.—These XVII expressions (fig. 8, e) I take to represent a development through **J** to **JK**, and the difference between this and the XVII major organ (d), as apart from size, is traceable to the curtailed development of III.

Antennal formulæ (including aberrant soldier antennæ of *T. bellicosus*):

Imago:

XIX : I II III (0000+17) IV (16) V (15) VI (14) VII (13);
fig. 7, a; fig. 8, a

Soldier:

XIX : I II III (0000+17) IV (16) V (15) VI (14) VII (13); fig. 7, b
XVIII : I II III (0000+17) IV (16) V (15+ 14) fig. 7, e, f
XVIII : I II III (0000+17 + 16) IV (15) V (14) fig. 7, c
XVII : I II III (0000+17 + 16) IV (15+ 14) V (13);
fig. 7, d, h; fig. 8, b

Major worker:

XVIII : I II III (0000) IV (17+16) V (15+14); fig. 8, c
XVII : I II III (0000+17+ 16) IV (15+14); fig. 8, d

Minor worker:

XVII : I II III (0000) IV (15+14); fig. 8, e

(5) *Odontotermes latericius* (*Haviland*). Fig. 9, a-m.

ANTENNAL INDEX.—Imago XIX; major worker XVIII, XVII; minor worker XVII; soldier XVII, XVI (XV).

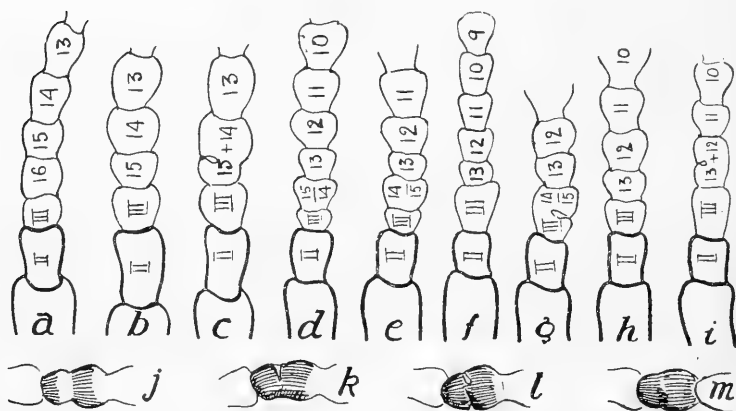
This is a species from which the major soldier caste appears to have been eliminated.

Imago.—The antennæ have been found to be regularly XIX-jointed (fig. 9, a) and are somewhat characterised by the shortness of joint III. Short as III is it may occasionally exhibit a notch on one side as it does in the antennæ of *T. bellicosus* and *natalensis*. This may be taken as indicating a suppressed tendency to be XX-jointed.

Major Worker.—The antennæ are of XVIII or XVII joints. The XVIII forms (fig. 9, *b*) are rarely met with, but express the full development of the organ for this caste. The XVII (*c*) are characterised by a gross or bilobate IV which represents a more or less complete fusion of IV, V of the XVIII organ—i. e. (15 + 14). Thus it may be a simple coarse joint or show any one of the phases represented by fig. 9, *j*, *k*, *l*, *m*.

Minor Worker.—These are XVII-jointed (fig. 9, *d*), and

TEXT-FIG. 9.



Odontotermes latericius (Hav.). *a*. Imago. *b*, *c*, *j*-*m*. Major worker. *d*. Minor worker. *e*-*i*. Soldier.

in them IV is always coarser than either III or V. It has, however, all the appearance of being a simple joint.

Soldier.—Only one soldier has been found with a pair of XV-jointed organs (fig. 9, *i*), in both of which IV was very noticeably compound. They are therefore to be regarded as aberrant reductions of the XVI expression (fig. 9, *h*) and due to the fusing of IV, V thereof—i. e. (13 + 12). There are three types of XVI-jointed organs: one (fig. 9, *h*) in which III is short, a second (fig. 9, *g*) in which it is longish and compound, and a third (fig. 9, *f*) in which it is longish and simple. The XVII-jointed organs (fig. 9, *e*) are characterised by the smallness of III and the grossness of IV; it is very

clear from their composition that the XVI organs, in which III is long, are due to the fusing III, IV of the XVII—i. e. (III + 15 + 14).

DEVELOPMENT.—The *ab ovo* expression is that of stage **A** (Pl. XV), joint III being in a trilobulate condition.

Imago.—These antennæ (fig. 9, *a*) seem to be derived from an uninterrupted development to **M** (Pl. XV), when either (16) abjuncts, as in **Nb**, or (17 + 16) abjunct, as in **MN**. I have not been able to decide which of the two courses is followed. The composition of the flagellum in either case is one of 21 elements, and in this respect is in agreement with those of *T. natalensis* and *bellicosus*.

Worker.—The XVIII-jointed antenna of the major (fig. 9, *b*) seems to result from a direct development to stage **K**, the XVII (fig. 9, *c*) through **J** to **JK**, the minor worker antenna (fig. 9, *d*) being a dwarfed form thereof. All these organs therefore have 19 elements to the flagellum.

Soldier.—The XVII organ (fig. 9, *e*) represents a development from stage **A** through **J** to **JK** and conforms with the worker XVII. The two XVI organs (fig. 9, *f, g*), in which III is elongate, simple or compound, illustrate a development to **J**, whilst the form in which III is short (fig. 9, *h*) is one which stops at **H**. The rare XV organs (fig. 9, *i*), on account of the length of III, are taken as developing from stage **A** through **G** to **GJ**. With the exception of the XVI regarded as an arrest of development at **H**, the remaining organs appear to have 19 elements to the flagellum, or two more than in the case of the arrested XVI.

Antennal formulæ :

Imago :

$$\text{XIX:} \begin{cases} \text{I II III(0000+ 17) IV(16) V(15) VI(14); or} \\ \text{I II III(0000) IV(17+ 16) V(15) VI(14)} \end{cases}$$

Worker :

$$\begin{array}{ll} \text{XVIII: I II III(0000)} & \text{IV(15) V(14) VI(13)} \\ \text{XVII: I II III(0000)} & \text{IV(15+ 14) V(13)} \end{array}$$

Soldier :

$$\begin{array}{ll} \text{XVII: I II III(0000)} & \text{IV(15+ 14) V(13)} \\ \text{XVI: I II III(0000+} & \text{15+ 14) IV(13)} \\ \text{XVI: I II III(0000)} & \text{IV(13) V(12)} \\ \text{XV: I II III(0000+} & \text{15+ 14) IV(13+ 12) V(11)} \end{array}$$

- (6) *Eutermes* (*Trinervitermes*) *trinerviformis et al.*
Fig. 10, *a-n*.

ANTENNAL INDEX.—Imago XVII, XVI, XV; major worker XV, XIV; minor worker XV, XIV; major nasutu XV, XIV, XIII; minor nasutu XIV, XIII, XII.

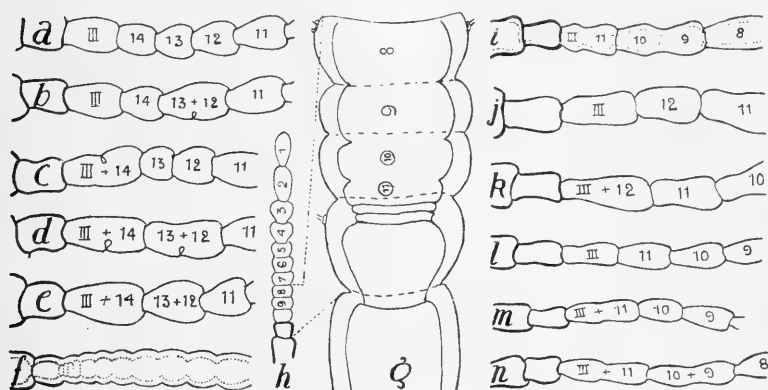
Covering the face of South Africa is an endless series of more or less similar mounds, the homes of very similar termites belonging to Holmgren's subgenus *Trinervitermes*. At one time or another these mound-builders have been mentioned in literature as the *Termes* (or *Eutermes*) *trinervius* of Rambur. That Rambur's insect occurs in South Africa is, however, extremely unlikely. If Sylvestri's account of Rambur's species is correct, the one first described by Haviland as *Termes trinervius Ramb.* and later by Sjostedt as *Eutermes trinervius (Ramb.)* is certainly not agreeable with the common Senegal form, and up to the present I have not succeeded in obtaining any local form that is. Among our South African *Trinervitermes* I recognise perhaps six which are sufficiently distinct. These can be broadly separated into two groups—those building cellular mounds, and those constructing hidden nests of a similar nature under stones. Apart from the intermingling of those belonging to one or the other of these two groups, each species tends to be restricted to areas which are not demarcated by land configurations, but rather by the predominance of certain grasses. Thus one, which will be referred to *Eutermes* (T.) *trinerviformis Holmgren*, although wide-spread, is confined to those parts of the country where the grass *Themeda forshalli* is dominant—in short, to that type of veld classed as “sour,” or which, with overstocking, tends to become sour.

Here I may explain that *Eutermes* (T.) *trinerviformis Holmgren* is identical with Haviland's *Termes trinervius Rambur*, and, further, is not separable from Holmgren's other Natal species *bulbiceps*, *auriceps* and *dubius*.

Imago.—Treated as a group the imago antennæ of the

Trinervitermes are either XVII-, XVI- or XV-jointed. It has never happened in my experience that all the winged individuals from a nest have antennæ of a regular number of joints. Those of trinerviformis are generally of XVII, but may be of XVI joints. Those of a species taken to be gemellus *Sjostedt* are generally XV, but may be XVI. Those of three undescribed species before me may be XV, XVI or XVII, and the common number varies with the broods of different nests.

TEXT-FIG. 10.



Eutermes (*Trinervitermes*) *trinerviformis* *Holmgren*. *a-e*. Imago. *f*. Larva of the third instar. *g, h*. Larva *ab ovo*. *i-n*. *Nasutu*.

The homologies of these variously composed antennæ is illustrated by fig. 10, *a-e*. The XVII is reduced to a XVI either by the union (13 + 12) as in fig. 10, *b*, or (III + 14) as in fig. 10, *c*. This again is reduced to a XV when both unions (13 + 12) and (III + 14) occur in the same organ as in fig. 10, *d, e*. There is seldom any trouble in establishing the compound nature of the conventional III or IV, as the case may be, as where they may appear simple, if large, as in fig. 10, *e*, another organ will show them pseudo-articulated as in fig. 10, *d*.

The development of these antennæ shows that in all patterns the flagellum is one of 19 elements. The XVII

organ illustrated by fig. 10, *a*, represents a development from **A** (Pl. XV) to **Kb** through **J**. The XVI organ shown in fig. 10, *b*, is a development from **A** to **GKb** through **G**, **GH**, **GJ**. The XVI of fig. 10, *c*, is a development from **A** to **J** with a tendency to arrive at **Kb**. The two XVI-jointed organs (*d*, *e*) result from a development through **G** to **GJ**.

The smallest nymphs (second instar) exhibit the XIV expression (stage **E**), and these progress through **G** either to **H** or **GH**, so becoming XVI- or XV-jointed. The nymphs of the final instar exhibit antennæ articulated like those of the imago.

Worker.—With both castes the antennæ are virtually XV-jointed expressions, such antennæ as count XIV being due to the fusing of III, IV of the XV. This in some cases is self-evident, especially in the antennæ of the major workers. In others it may not be so clear, and in many minor workers the XIV expression exhibits a simple rather than a compound III. The development of the organ is from stage **B** (Pl. XV) to **E** and this is the condition after the third ecdysis. In this stage the flagellum contains 15 elements, as in the third instar (fig. 10, *f*'), four of which are compressed more or less into III. Of these the more distal, the element of (12) is the most developed, and it depends upon the extent of its development whether the organ remains XIV- or becomes pseudo- or actually XV-jointed. The variable length of III which obtains with different species or with the same species, especially with the incipient and juvenile forms, depends upon the development of the elemental region of such an organ as that represented by fig. 10, *f*.

Nasuti.—In his synopsis of the sub-genus *Trinervitermes* Holmgren gives the number of joints for nasuti antennæ as XII, XIII and XIV. As I have obtained ordinary and pteroergate nasuti of *T. trinerviformis* with XV-jointed antennæ, the synopsis needs to be extended to include these forms.

Some authors give the joints as XII or XIII and as XIII or XIV, and occasionally it may be gathered from the description

that when XII-jointed both III and IV are long joints, or when XIII or XIV-jointed III is long in the XIII and short in the XIV expression; some go so far as to state that the XIII expression is due to the failure of III and IV of the XIV to separate. Generally, however, the descriptions are not very illuminating.

In the case of *trinerviiformis* the length of III in a XIV expression may be very variable, as it depends upon the age and activities of a particular community what the development of III is. Similarly it depends upon the age and prosperity of the community what the segmentation of the organ is. In short, with this species the antennal features of the *nasuti* depend to an extraordinary extent upon the nutritive factor. Thus in very young colonies XII and XIII-jointed antennæ are the more common, in older, XIII and XIV; whilst, in established and prosperous communities, XIV prevails and may be accompanied by XV, especially with large individuals.

The antennæ *ab ovo* are definitely XII-jointed and in stage **B**. Their condition remains the same until after the first ecdysis, and is as illustrated by fig. 10, *g, h*. At this stage the flagellum is composed of 10 joints with the elements of 4 in the formative zone. After the second ecdysis the antenna is XIV-jointed as in fig. 10, *f*; there being 12 joints in the flagellum with the elements of 4 in the formative (stage **E**). The final antenna depends for its form upon the developments of the third instar, and these may range from stage **E** to **G**, the potential XVI-jointed pre-stage of **H**.

In the progress of the third period of quiescency certain changes take place, and with the ecdysis the organ virtually acquires its adult expression. The elemental subdivisions in III fuse to form a homogeneous whole or core.

Small-sized *nasuti* will present, in the callow stadium, antennæ of the type represented by fig. 10, *i*. This, according to the developed articulations, is a XII-jointed organ, and is so because two articulations have become suppressed, one between (9) and (10), another between III and (11). The

suppression of the articulation as between III and (11) is a very common occurrence with termite antennæ, and constitutes the feature, already alluded to, which transforms an organ with a potential even number of joints into an odd-jointed expression. The suppression of the articulation between the non-sister joints (9) and (10) is an extraordinary condition even as a result of dwarfing. From the internal condition of the organ, represented by fig. 10, *i*, it can be seen that it is a potential XIV expression, or XIII, according to whether both or one of the suppressed articulations have developed sufficiently before the mutation occurred. Should both develop, a XIV organ results in which III and IV are about equal; if only that between (9) and (10), a XIII organ in which III is decidedly longer than IV. Such XIII and XIV organs characterise the nasuti belonging to more or less juvenile communities, whilst the XIV and XV expressions of populous and prosperous communities, in which III is a longish joint, follow upon a greater degree of antennal development. In figs. 10, *j*, *k*, *l*, *m*, *n*, the homologies of the main forms are indicated. Figs. *j* and *k* illustrate the XV and XIV expressions of large-sized major nasuti. Figs. *l* and *m*, the XIV and XIII of minor nasuti found in mature colonies. Fig. *n* represents the XII-jointed organ of nasuti belonging to an incipient community.

(7) *Rhinotermes putorius* *Sjostedt*. Fig. 11, *a-k*.

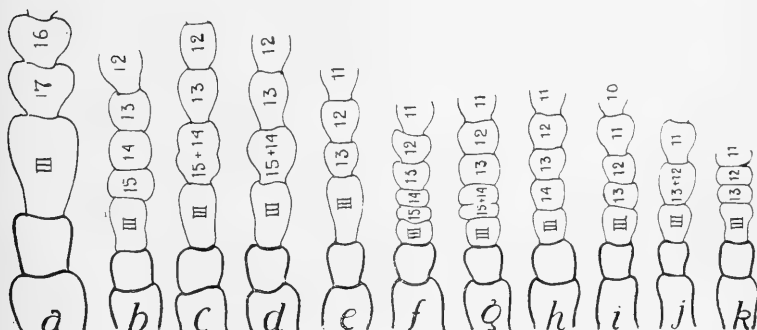
ANTENNAL INDEX.—Imago XX (XXI); major worker XVIII, XVII; minor worker XVI (XVII); major soldier XVIII, XVII (XVI); minor soldier XVI, XV.

The development of the antennæ of this species has not been extensively examined. The smallest larvæ, probably of the first instar, were found to have organs in stage **A** (Pl. XV), while some larger individuals had organs in stage **D**. The antennæ of imago-nymphs of the fifth instar are of XX or XXI joints; in both forms III is an enlarged joint as in fig. 11, and, in the XX expression, exhibits a distinct annulation—a feature disappearing with chitinisation.

Imago.—In view of the absence of any compound joint in the flagellum of the XX imago organ (fig. 11), its development appears regular from stage **A** to stage **P**. Later it may reach the stage **Pb**, when, by the exceptional abjunction of (18) as an orphan-joint, a XXI-jointed organ originates. The III of the XX expression may well be regarded as comprising 6 joint-elements showing the flagellum to comprise 23 elements.

Major Soldier.—Ordinarily the antennæ are XVII-jointed (fig. 11, *d*), IV being a little coarser than either III or

TEXT-FIG. 11.



Rhinotermes putorius Sjostedt. *a*. Imago. *b, c, d, e*. Major soldier. *f, g*. Major worker. *i, j*. Minor soldier. *k*. Minor worker.

V. In most there is little else than its coarseness to indicate IV as a compound (15+14); this is, however, revealed in the organ represented by (*e*), which happened to be the companion of that of (*d*). The XVII is therefore derived from the XVIII, (*b*), by the (15+14) combination; but in view of the greater length of III in these expressions, the XVIII-jointed organs appear to be arrested at stage **K**, and the XVII at stage **JM**. Therefore, in the XVIII expression, III comprises 4 elements and, in the XVII, 6 elements, thus illustrating a greater development although the total of joints is less.

One major soldier was found with both antennæ of XVI joints (fig. 15, *e*), and from the condition of III this is regarded as the result of arrest on reaching stage **J**.

Minor Soldier.—The antennæ are XVI- or XV-jointed (fig. 11, *i, j*). The two forms having been found as companions upon one insect, it is very clear that the XV is derived from the XVI as the result of a (13+12) union. The shortness of III indicates that one is arrested at stage **H**, the other at **GH**. The flagellum is therefore one of 17 elements.

Major Worker.—The antennæ of the major worker are usually XVII (fig. 11, *h*), but may occasionally be XVIII-jointed (*f, g*). These organs seem to illustrate two stages of development. The XVIII expressions represent stage **K** when the flagellum is one of 19 elements. From the general appearance of the XVII organs they seem to represent stage **Kb** and are XVII by the abjunction of (14). Such antennæ would have the same elements in the flagellum but the formative not so developed. Alternatively IV may be a dwarfed (15+14) compound.

Minor Worker.—These organs count either XVII or XVI. The XVII represents a development to stage **Kb**. The XVI (fig. 11, *k*) is a development which ceases as between **I** and **J**, and in both expressions the elements of the flagellum may be regarded as 19.

Antennal formulæ :

Imago :

XXI : I II III (0000) IV (18) V (17) VI (16)

XX : I II III (0000 + 18) IV (17) V (16); fig. 11, *a*

Major soldier :

XVIII : I II III (0000) IV (15) V (14) VI (13) VII (12)

XVII : I II III (0000 + 17 + 16) IV (15 + 14) V (13) VI (12)

Minor soldier :

XVI : I II III (0000) IV (13) V (12)

XV : I II III (0000) IV (13 + 12)

Major worker :

XVIII : I II III (0000) IV (15) V (14) VI (13) VII (12)

XVII : I II III (0000 + 15) IV (14) V (13) VI (12)

Minor worker :

XVII : I II III (0000 + 15) IV (14) V (13) VI (12)

XVI : I II III (0000 + 15 + 14) IV (13) V (12)

(8) *Calotermes durbanensis* Haviland. Fig. 12, *a-h*.

ANTENNAL INDEX.—Imago XIX to XV; soldier XV to X.

As indicated by the index the final antennæ of this species are an epitome of variation and of oddity. An examination of undifferentiated larvæ and of later developing forms conveys the impression that the joints are abjuncted in the usual manner. Those of the undifferentiated may be X, XI, XII, and those of small forms with discernible wing-sacs may be XII, XIV, XV. The largest nymphs usually exhibit antennæ of XVII, the common quota of the organs of the imago. No XIX-jointed nymphs were found, and this is to be attributed to the comparative rarity of final organs with so many joints. The following table shows the variation for the series examined:

Imago.			Soldier.		
XIX - jointed antennæ	.	8	XV - jointed antennæ	.	2
XVIII	" "	21	XIV	" "	15
XVII	" "	27	XIII	" "	41
XVI	" "	10	XII	" "	31
XV	" "	1	XI	" "	5
			X	" "	1
Total . . .			Total . . .		
67			95		

In all soldier antennæ joint III is extraordinarily large and clavate: it is such that it seems to foreshadow III of the three-jointed scape of specialised insect-antennæ. In some of the XVI and XVII imago antennæ III also tends to be gross and clavate, but never so strikingly as is the case with the soldier.

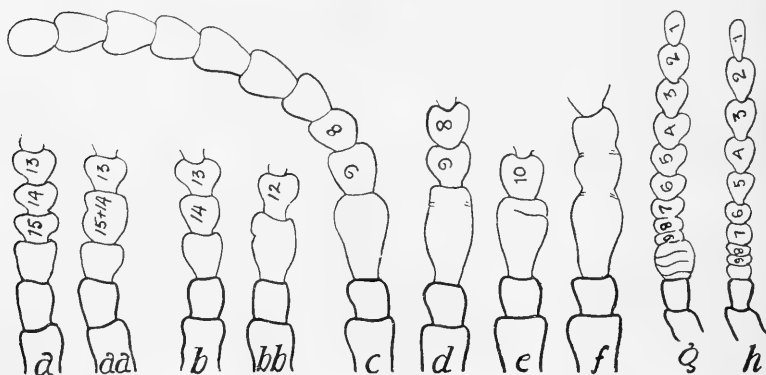
Imago.—The imago antennæ group themselves into two series: (i) those that develop along the lines of stages **A** to **Nb**, when (16) is abjuncted and they become XIX-jointed; (ii) those suffering arrest, which, whilst it does not interfere with the development of elements, does interfere with that of

articulations, so that the elements fuse and a longer or shorter joint forms about different totals of elements.

A pair of antennæ is illustrated by fig. 12, *a-aa*, of which one is XVIII-jointed, and the other, owing to a (15 + 14) union, XVII-jointed. Another pair is illustrated by (*b-bb*), one of which is normally XVII, whilst the other is XV-jointed; as between these two organs a considerable disparity will be noticed in joint III.

With a view to ascertaining whether any relationship existed between the length of III and the supposed number of

TEXT-FIG. 12.



Calotermes durbanensis Haviland. *a, b*. Imago. *c-g*. Soldier.
h. In second instar.

joint-elements it comprised the basal joints in the flagellum of four antennæ were measured. The results are shown in the following table, the length units being micro-ocular divisions.

The proportions are seen to be peculiarly regular, especially the 10, 14, 18 series. That III in the XIX expression is slightly out of proportion is due to the condition of the elements it represents.

XIX:	III = 8	IV = 6	V = 6	VI = 8	VII = 8	VIII = 10	IX = 10
XVIII:	III = 10	IV = 8	V = 8	VI = 8	VII = 10	VIII = 10	
XVII:	III = 14	IV = 8	V = 8	VI = 10	VII = 10		
XVI:	III = 18	IV = 8	V = 10	VI = 10			

The homologies of the antennæ may be formulated as follows :

XIX : I	II	III (0000+15)	IV (14)	V (13)	VI (12)	VII (11)
XVIII : I	II	III (0000+15+	14)	IV (13)	V (12)	VI (11)
XVII : I	II	III (0000+15+	14+	13)	IV (12)	V (11)
XVI : I	II	III (0000+15+	14+	13+	12)	IV (11)

It would seem, therefore, that the distinctions are not due to the development of the organs being arrested in an earlier stage, but to the failure of articulations to come into evidence, so bringing about the fusing with III of rudimentary joints.

Soldier.—The antennæ of soldiers invariably exhibit the peculiar grossness and clavate shape of III; they differ in the number of articulated joints in different individuals and on the two sides. The details of variation are given in the accompanying table :

Symmetrical pairs.			Asymmetrical pairs.		
XII joints . . .	9	soldiers	XI and XIII joints . . .	1	soldier
XIII „ . . .	9	„	XII „ XIII „ . . .	2	soldiers
XIV „ . . .	5	„	XIII „ XIV „ . . .	1	soldier
			XIII „ XV „ . . .	1	„
			XIV „ XV „ . . .	1	„

The various antennæ are represented in fig. 12, *c-f*. As there is no decided difference in the length of III throughout the series, fig. 12, *c*, is representative of all except such in which III is noticeably compound as in (*d*) and (*e*), or in which a long fused joint has formed about III, IV and V, as in (*f*). It seems highly probable from the condition of the organ of a wingless form, possibly a third instar soldier, represented by (*g*), that joint-multiplication subsides at different stages and is replaced by modification; ergo, the dilation of III is due to the increase in the transverse dimensions of the elements instead of one in their axillary dimension.

(1) Development.—The *ab ovo* expression is somewhat

variable, but may be described as an VIII rising to X. In the second instar it is XII (fig. 12, *h*).

The variableness of soldier antennæ may be attributed to the subsidence of joint-multiplication in both the second and third instars ; but why, in some cases, one antenna should be affected earlier than its companion cannot be any more readily explained than why both of one insect should be earlier affected than both of another, unless the asymmetry of the antennæ of the two sides arises from asymmetrical castration.

The rare X-jointed organ represents a development in which no annulations are formed after the first instar, i. e. at stage **A**, whilst the XV-jointed represents a development beyond stage **G**.

(9) *Cryptotermes* *sp.* Fig. 13, *a-h*.

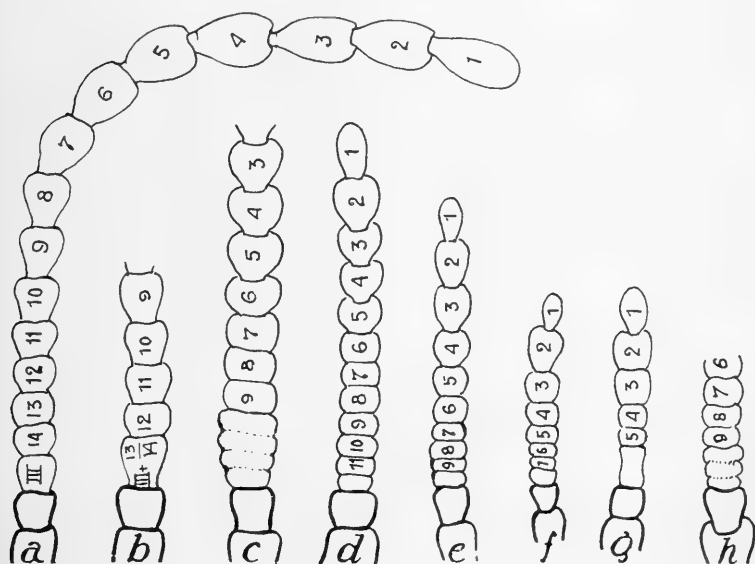
ANTENNAL INDEX.—Imago XVII, XVI, XV ; soldier XV, XIV, XIII, XII, XI.

This is a fairly common species ranging along the littoral of Natal. It may or may not be a described form. It is one from which the soldier caste seems to be in the process of elimination, as I only succeeded in obtaining 21 examples from four communities.

The specialisation of the soldiers, as apart from features of reduction, may be described as an extraordinary degree of cephalisation, and this has a very decided influence upon the form of the final antennæ. The basal section of the flagellum is composed of an ill-defined series of annulations, and its condition is such that it foreshadows the form of the long III in the antennæ of *Calotermes durbanensis*. Further, it renders any counting of the joints unsatisfactory. Fig. 13, *c*, represents a fairly well-defined organ of XV joints ; in many, however, the definition is not so good. With most the apical series (1) to (9) become well-defined and seem to represent a development to **D**. Any antenna of apparently less than XII joints may be regarded as arising from the fusing of (9) with the rudimentary series.

Imago.—The variation given for the imago in the antennal index is based upon the examination of 49 organs. These represented 19 pairs and 11 single organs. Of the pairs, 4 were asymmetrical, 3 being XVI-XV and 1 XV-XII. The last mentioned, XII, is only recorded as a matter of interest, as it was essentially aberrant and probably owed its

TEXT-FIG. 13.



Cryptotermes sp. *a-b*. Imago. *c*. Soldier. *d-h*. Developing antennæ origin to some injury—a most unusual factor. The table shows the preponderance of the XV- and XVI-jointed organs.

No. of joints .	XII	XIII	XIV	XV	XVI	XVII
No. of antennæ .	1	0	0	25	21	2 = 49

All arise from the phase of the nymphal antenna (fig. 13, *d*), which is about in stage **E** (Pl. XV). If this develops to **G** and (12) is abjuncted the XV organ results; if (12) and (13) abjunct the organ is XVI-jointed (stage **H**). Should any development

beyond **H** take place the organ will, by progressing to **Kb** through **J**, become one of XVII joints.

DEVELOPMENT.—The condition *ab ovo* (fig. 13, *g*) may be regarded as one of VIII progressing to X, as in (*f*). This becomes XII as in (*e*), and this XIV as in (*h*). (Figs. 13, *d-g*, are in proportion.)

(10) *Psammotermes allocerus* *Silv.* Fig. 14 *a-w*.

ANTENNAL INDEX.—Imago XVI; soldier XVI to X; worker XVI to XIV (XVII).

This is essentially a desert termite¹ presenting many peculiarities, some of which at least may yet be traced to its evolution in fitting itself to the conditions of an adopted environment.

The imagos are small; bulk for bulk they are larger than the rank and file of the community, but there are always a good many soldiers larger, and a small percentage particularly so.

The workers do not attain a distinct adult appearance, but this seems only because they do not become strikingly pigmented. Their colour is cream compared to the milk white of the immatures. There is no special caste distinction, and they range from small to large in a finely graduated series. A few workers are comparatively large, but not bulkier than the imagos.

The soldiers are extremely variable in size; the smallest lesser than the imagos, the largest greater. As with the workers they also intergrade finely with a few which seem exceptionally large, as against the majority in a given nest series. This is brought out in the following table of 67 head-widths for one nest series, as in this species the head-width of the soldier is closely in proportion with the length and

¹ Holmgren, Nils ("Termites from Natal and Zululand," 'Entomol. Tidskrift,' Arg. 34, Haft 2-4) reports *Psammotermes fuscifemoralis* *Sjostedt*, a species of the littoral of the Red Sea, as being obtained by Ivar Trägårdh in 1905 at Lake Sibayi, in Zululand. This record as regards the locality needs confirmation.

bulk of the body. The break in the series will be observed to occur between 0.75 and 0.84 mm., and it will be seen that practically half of the soldiers were of the intermediate size.

Head width mm.	0.45	0.48	0.51	0.54	0.57	0.60	0.63	0.66	0.69	0.72	0.75	0.78	0.81	0.84	0.96	0.99
No.	4	3	5	7	4	6	23	5	1	2	4	0	0	1	1	1

It is not usual among termites for the soldiers and workers to be decidedly larger than the imagos, and therefore the exceptionally large soldiers of *P. allocerus* may be atavistic, and indicate the evolution of the species from a larger ancestor. Further, in those species where the soldiers and workers approach the size of the imagos, and even with some where both soldiers and workers are relatively small, larger individuals may exhibit antennæ of more joints than do their lesser companions. This is not the rule with this *Psammotermes*. It is true that the largest individual measured possessed antennæ of the same number of joints as the imago (fig. 14, *i*), but the others had fewer, and there is little relationship between the size of the individual and the number of joints in their antennæ.

The range given in the antennal index for the soldier caste is based upon a count made of the number of joints in 91 antennæ. This on analysis showed XIV to be the common expression, but there were many of XII, XIII and XV.

No. of joints	...	IX	X	XI	XII	XIII	XIV	XV	XVI	
No. of individuals	...	1	1	6	18	15	39	10	1	=91

Generally companion antennæ are composed of the same number of joints, but asymmetrical alliances are quite frequent, the combinations met with being XV-XIV, XV-XIII, XIV-XIII, XIV-XII, XIV-X and XII-XI (see fig. 14, *k*, *l*, *n*, *o*, *g*, *s*).

Nearly all soldier antennæ agree as regards their pattern and are characterised by a swollen joint, III, and depart

widely from the larval pattern, which is retained more or less by the imagos and workers. There are exceptions, however, as in the organs of the smallest soldier found (fig. 14, *t*). When each of a pair of antennæ are composed of the same number of joints they are always more or less dissimilar in detail, and the pair represented in part by (*p-pp*) are recorded for their conformity as regards the basal series of joints. The only statement which can be made and which appears to hold good very often is that when there is a difference of one joint, joint III of the lesser expression is as long as III + IV of the greater; but there are exceptions, as may be noticed by comparing the pair represented by fig. 14, *n-nn*. One would expect to find III disproportionately large where the difference runs to two joints but this is not the case (cf. (*o-oo*) and (*q-qq*)). On the other hand joint III is a compound joint, and is made up in some cases of three or four or more joints. In all antennæ it is the repository of a number of joint-elements.

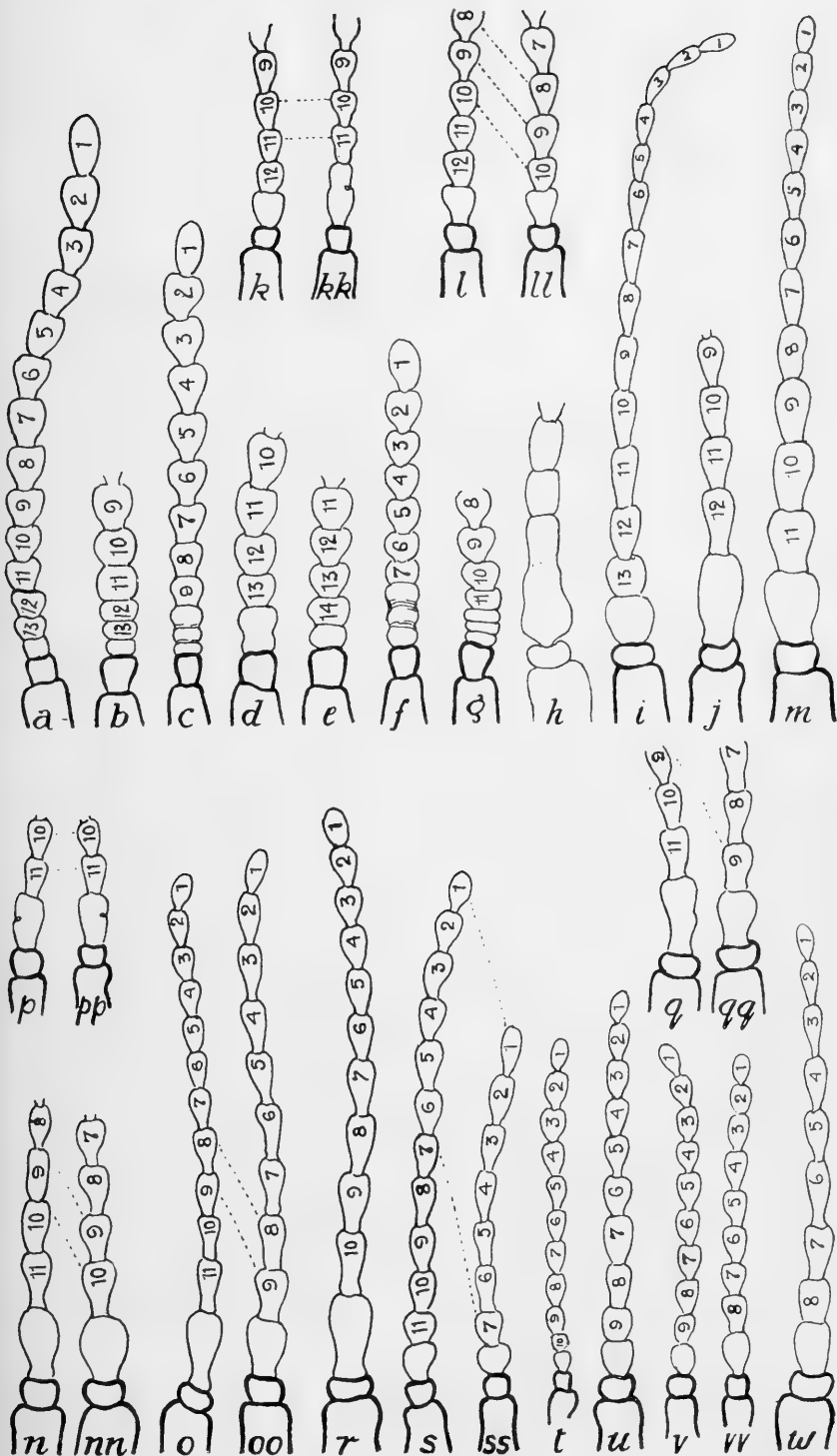
Unfortunately the material before me contains very few immature forms of any sort, but in a series of callow soldiers of the fourth instar the antennæ (fig. 14, *h*) show the formative zone and the more recently formed joints to be swollen and wider at the base than at the apex—a quite opposite condition to their final form.

To summarise, the process of joint-multiplication with soldiers is determined in a very erratic manner and its subsidence is followed by a very distinct modification. Modification possibly arises to a more or less marked extent in the third instar, becomes pronounced in the third period of quiescence and has certain changes in the fourth instar.

Development.—The development of these antennæ follows the common process whereby two sister-joints are abjoined at a time. The youngest forms examined have organs (fig. 14, *f*) in stage **B** (Pl. XV). The imago antennæ (*a*) are regularly XVI-jointed, but III is slightly variable in length

TEXT-FIG. 14.—*Psammotermes allocerus* Silv. *a, b*. Imago.
c-e. Worker. *f, g, h*. Developing antennæ. *i-w*. Soldier.

TEXT-FIG. 14.



and in some exhibits a faint pseudo-articulation. It is regarded as a regular development to stage **H**. The nymph of the last instar also has XVI-jointed antennæ (*b*). All the worker antennæ may be classed as regular developments to stage **E** or to **I**, with an occasional tendency to pass through **J** to **Kb** and so become XVII (fig. 14, *c-e*).

With reference to the asymmetry in the pairs of soldier antennæ, the most extraordinary seen is that represented by fig. 14, *s-ss*. The X-jointed expression is aberrant; it is not aborted, but an organ in which joint-multiplication has subsided when in stage **A**. It is one of X joints, but with a flagellum of quite 13 elements. Its XIV companion may only be regarded as one that developed either to the stage **F** or **G** with a flagellum of 17 elements. If it could be shown conclusively that the multiplication of joints in the termite antenna was correlated with the development of the organs of reproduction, the asymmetry of these soldier antennæ might be traced to an asymmetrical degeneration and atrophy of the organs of sex—i. e. asymmetrical castration.

(11) *Cubitermes* (*bilobatus* group).

ANTENNAL INDEX.—Imago XVI, XV; worker XV, XIV; soldier XV, XIV.

The antennæ of the three castes are the outcome of a very short course of joint-multiplication. The smallest undifferentiated forms exhibit the pseudo-XII expression (stage **A**), in which the flagellum is composed of 13 elements. The XIV-jointed worker and soldier antennæ are both developments to the stage **F**. The XV organs, in which III, IV and V are subequal, are arrived at by the subdivision of III, (12) being abjuncted. The XV antenna of the imago and some workers, in which III is small and IV relatively large as compared to either III or V, represents a development to stage **GH**, the coarse IV being a (13 + 12) combination.

(12) *Microcerotermes* (parvus group).

ANTENNAL INDEX.—Imago XIV, XIII; soldier XIII; worker XIII (XII).

The ab ovo expression of the antennæ of this group is stage **A**. They are X expressions in which III is triloculate.

The XII-jointed worker organs represent a development to stage **C**, and there is usually a faint articulation in III illustrating a development towards **D** by the abjunction of (10). The XIII expressions of the soldier and workers represent a development to stage **Db**.

The antennæ of the imago are usually XIII-jointed. In them III may show a small, clear ring of chitin, a mere vestige of a pseudo-articulation, or it may exhibit an annulation near its base. The XIV organs are rare and characterised by a minute III. Both XIII and XIV represent a development through **D**, the XIII being derived by the abjunction of (10) (stage **Db**) and the XIV by the subdivision of III into three joints (stage **F**).

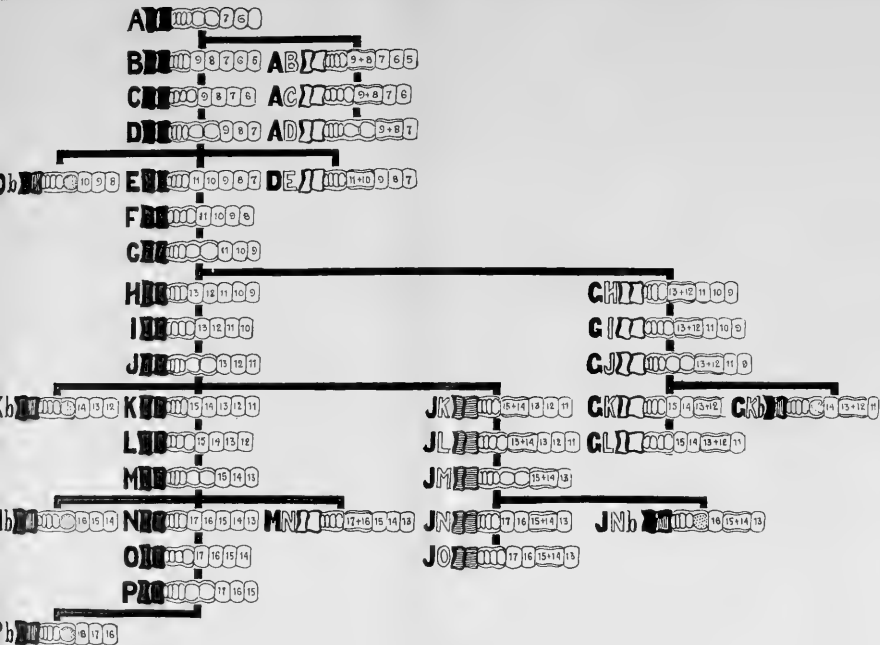
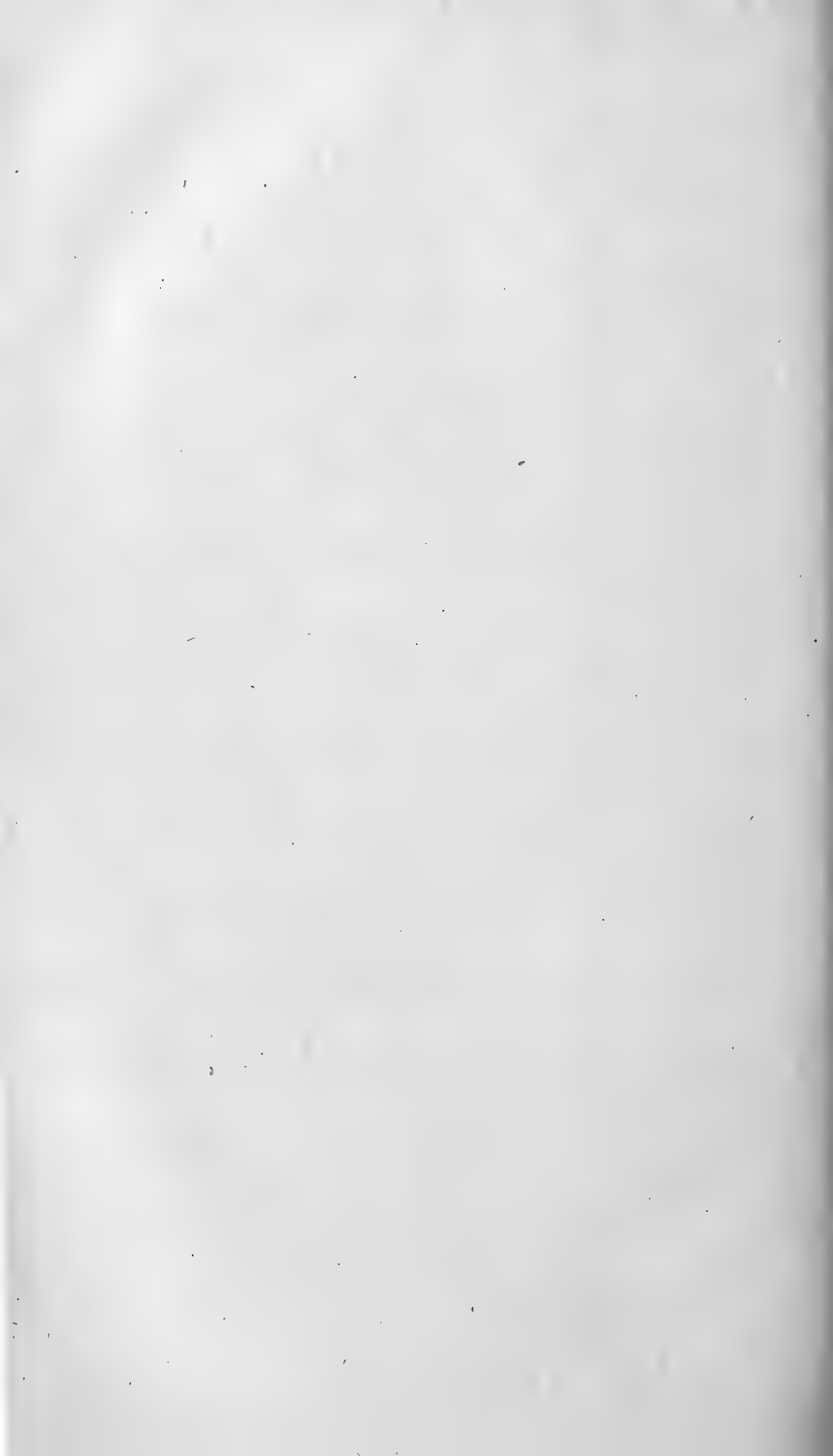


CHART ILLUSTRATING JOINT-FORMATION IN THE ANTENNA OF TERMITES

The outlined letters in this Chart are represented by italic capitals in the text references



Observations on the Comparative Anatomy of
the Termitophilous Aleocharine Paracoro-
toca akermani (*Warren*).

By

Ernest Warren, D.Sc.(Lond.)

With Plates XVI—XXI, and 5 text-figures.

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INTRODUCTION.

IN 1914 the writer gave a brief diagnosis of a new termitophilous Aleocharine Staphylinid from Natal.¹ The beetle is extremely physogastric, and it was referred to the remarkable American genus *Corotoca* and named *C. akermani*. A more detailed examination of the species, however, has brought to light certain differences, and it is now thought to be advisable to found a new genus which, on account of its great external similarity to *Corotoca*, is named *Paracorotoca*.

In the present paper the anatomy and histology of *Paracorotoca akermani* (*Warren*) is given in certain detail on account of the fact that hitherto only a brief description of the external morphology of the similarly modified genus *Corotoca* has been published.² In order to appreciate fully the nature of the modifications induced by the termitophilous habit in *Paracorotoca* a full knowledge is required of the structure of the most closely allied free-living genera of Aleocharine Staphylinids. I have been unable to trace any very helpful literature in this connection, and consequently for the present the significance of some of the anatomical characters must remain doubtful.

A comparison of the anatomy of *Paracorotoca* with that of Trägårdh's *Termitomimus entendveniensis*³ from

¹ Warren, E., "Note on the Occurrence in South Africa of a Termitophilous Beetle of the Genus *Corotoca*," 'Ann. Natal Museum,' vol. iii, pt. i, p. 103, 1914.

² Schiödte, J. C., 'Corotoca og Spirachtha,' Kjobenhavn, 1854.

³ Trägårdh, Ivar, "Description of *Termitomimus*, etc.," 'Zoo. Stud. titlag. T. Tulberg,' Upsala, 1907.

Zululand has considerable interest, but we are confronted with the difficulty as to whether certain resemblances are to be regarded as indicating genetic affinity, or convergence of structure arising from the effect of the same environment, since the two termitophiles inhabit the nest of the same species of termite. Some light, however, is thrown on the matter by a general comparison of the modifications of the termitophilous insects.

In external appearance *Paracorotoca akermani* closely resembles *Corotoca melantho* *Schiödte*, from Brazil, but in the characters of the mouth-parts it shows a closer affinity to *Termitoptochus indicus* *Silv.* from Singapore, and in internal anatomy there is a marked similarity to *Termitomimus* of S. Africa.

I. OBSERVATIONS IN THE FIELD.

HABITAT.—*Paracorotoca akermani* has been found only in the nests of the common *Eutermes* of Natal. This termite is usually known as *Eutermes trinervius* (*Ramb.*), but Mr. Claude Fuller, who is studying the subject, informs me that the insect is really *Eutermes trinerviformis* *Holm.*

Dr. Conrad Akerman, after whom the species is named, discovered the first specimen near Pietermaritzburg in March, 1913. Subsequently he obtained further material, and it is through his kind assistance that a sufficient number of specimens have been available for this investigation. The beetle is exceedingly scarce and excessively troublesome to find, and even now, after the expenditure of much energy, the field observations are far from complete, since the pupa stage has not been found, and none of the female specimens exhibited the viviparous development of young. It is inherently probable, however, judging from the internal anatomy, that *Paracorotoca* resembles *Corotoca* in being viviparous.

In March, 1915, without a knowledge of Dr. Akerman's discovery, Mr. David Boyce of the Durban Museum found three specimens of *Paracorotoca* in a *Eutermes* nest near

Durban. These specimens have been kindly submitted to me by Mr. E. C. Chubb, Curator of the Museum, and they certainly belong to the species *P. akermani*.

Subsequently I was informed (in litt. 27/3/15) by Dr. F. Silvestri that he had found a similar termitophile in the nest of *Eutermes trinervius* in West Africa; quite possibly this also is *akermani*.

The specimens found in Natal are the following :

Environs of Pietermaritzburg: Durban Road (Akerman), one specimen, March, 1913; Botanical Gardens (Cullingworth), one, July, 1913; Zwart Kop Road (Warren), one, July, 1913; Bisley Road (Warren), one, December, 1913; Town Hill (Akerman), five in one nest, September, 1917.

Natal Coast: Durban (Boyce), three in one nest, March, 1915; Winkle Spruit (Akerman), two in one nest, May, 1917.

Of these 14 I have examined all but one. There were three undoubted males, 6 undoubted females, and the sex of the remaining 4 could not be determined without mutilation.

It was in June, 1905, that Dr. Trägårdh found numerous specimens of his *Termitomimus entendveniensis* in *Eutermes* nests in Zululand, and from his published account of the anatomy it will be seen that this beetle bears some striking similarities to *Paracorotoca akermani*.

In June, 1916, I found many specimens of *Termitomimus*, belonging undoubtedly to Trägårdh's species, in the nests of *Eutermes trinerviiformis* Holm. in a restricted area in the environs of Pietermaritzburg, and subsequently Dr. Akerman found the same species in a neighbouring locality.

The pupæ of *Paracorotoca* and *Termitomimus* are unknown, but certain Staphylinid larvæ modified in a termitophilous manner have sometimes been found fairly abundantly in the nests in which adult *Paracorotoca* occurred; also, one specimen of a somewhat differently shaped Staphylinid larva was discovered in a nest containing numerous adult *Termitomimus*. There would seem to be little doubt that these larvæ may be referred to the two physogastric beetles,

although in the absence of developmental stages and pupæ these determinations lack absolute certainty. I feel some confidence in the matter, however, from the fact that only these two termitophilous Staphylinid larvæ have been found, although hundreds of *Eutermes* nests have been examined, and it might be reasonably expected that if they were the larvæ of other termitophilous beetles the adults would also have been discovered. The larvæ are of appropriate sizes, and in the case of the supposed *Paracorotoca* larva there is a certain resemblance to a somewhat obscure figure by Schiödt of the reputed larva of *Corotoca melantho*.

The *Paracorotoca* larva is exceedingly delicate, and soon dies under all the various artificial conditions that have been tried. It must be mentioned that the larva is very much more abundant than the adult beetle. Possibly the presence of quiescent pupæ is misunderstood by the termites, and they may interfere with them injuriously.

HABITS.—From the nature of the case it has unfortunately not been possible to ascertain many details as to the mutual relationships between the termitophile and the termites.

When the living beetle is placed in a tube with some pieces of nest-material and a number of workers and soldiers, no obvious attention or solicitude on the part of the termites is noticed, but the presence of light and the untoward surroundings may sufficiently account for the apparent indifference.

A very interesting observation, however, has been made by Dr. Akerman, and subsequently both Mr. Boyce and I have witnessed similar occurrences. When termites are in any way alarmed, as by opening the nest or by sudden exposure to light, they vibrate their bodies in a very characteristic manner, and the beetle acts in a similar way. It is extremely doubtful if this vibration of the body is a common habit among free-living Staphylinids, and almost certainly it has been in some way acquired by the beetle through its association with the termites. It is not easy to see that the habit of vibrating the body can be of any actual utility to the termite, although possibly it may frighten small enemies;

and soldiers when alarmed often tap their mandibles against the ground with considerable force. Whatever its origin, the habit is now mainly a reflex action, and may be compared with the trembling with rage or fear in the higher mammals. In the case of the beetle it seems very doubtful if the habit could be acquired for the purpose of deceiving the termite host. It is easier to suppose that the intimate association of the beetle with the termites in the confined environment of a termite nest has produced in it a similar nerve tone.

The adult beetles are usually found in the more peripheral nest-galleries in company with a great crowd of adult workers and soldiers, while on the other hand the supposed *Paracorotoca* larvæ have always been found in the central portions of the nest, living amidst a close assemblage of immature termites and developing eggs. In the case of the larva, vibration of the body has not been noticed, and the legs are relatively short and weak.

In general shape, size and colour the adult beetle, with its forwardly directed abdomen, is not unlike an adult worker-termite or young nymph, but the resemblance is not so striking as to deceive readily the trained eye. Also, the legs of the beetle are long, and the insect is as active as the adult termites. The *Paracorotoca* larva has short legs and is slow in movement. In movement, general shape and appearance it resembles rather closely the immature termites amongst which it is living. On the whole it would appear probable that the resemblance is not entirely accidental, but has been partly acquired for the sake of giving a familiar, non-aggressive aspect to the guest, and thus rendering it acceptable to the host.

No direct observations on the feeding habits of the beetle have been possible. It will be seen that the hinder portion of the pharynx is entirely suctorial in character, and no solid matter has ever been seen in the gut. On the other hand, the mandibles are well-developed both in the larva and in the adult; they are large, smooth, pointed structures without teeth or serration of any kind. They could have no very

efficient masticatory function, but they could be used as powerful pincers. If the larvæ and adult beetles subsist entirely on fluid food supplied voluntarily by the worker-termites we might expect that some degeneration of the mandibles would have occurred. From these considerations it would seem probable that any fluid food that may be supplied by the termites is insufficient for the vital activities of the beetle, and is supplemented by an occasional suck of the body-fluids of the immature termites. It should be noticed that similar, powerful, pointed mandibles are present in the allied genera of termitophilous Staphylinids, e.g. *Termitoptochus*, *Termitomimus* and *Termitobia*.

The remarkably swollen abdomen of *Paracorotoca* is turned upwards and forwards, and extends as far as the middle of the prothorax. The morphological dorsal surface of the abdomen is especially modified for resting on the dorsal surface of the elytra, which are well adapted for supporting the heavy, inflated structure. The alæ are quite rudimentary.

In the living beetle the abdomen possesses considerable power of movement, and sometimes it may be stretched backwards almost in line with the head and thorax. This position is a strained one, and obviously requires much muscular exertion.

Many Staphylinids possess the power of turning their abdomen forward over the thorax, and the *Corotoca*-condition may be regarded as an extreme exaggeration of this power.

As we shall see subsequently, the main bulk of the inflated abdomen in both male and female is occupied by the greatly hypertrophied sexual organs. There is a considerable amount of fat-tissue, but the characteristic feature of the abdominal organs is the great size of the reproductive apparatus. In the case of the female this is not due to any exceptionally large number of ova, but to the relatively huge size of the individual eggs filled with large yolk-globules. The large size of the eggs is almost certainly associated with a viviparous

habit and the production of relatively large larvæ. Out of scores of larvæ collected at different seasons of the year from a considerable number of termite nests the smallest specimens found measured at least .75 mm. in length, and we may plausibly suppose that very minute larvæ would not have sufficient strength to obtain the requisite food in the nest of the termite.

It is less easy to interpret the reason for the great hypertrophy of the testes in the male. The vesiculæ seminales hold a very large amount of semen—sufficient, in fact, to fill scores of spermathecæ. In the majority of insects the male copulates once only and then dies. It is doubtful as to how far male beetles may be capable of repeated copulations; but there can be no doubt at all that in the present case the production of semen is very greatly in excess of actual requirements. The meagre material collected tends to point to a predominance of females (6 undoubted females and 3 undoubted males), but the amount of semen present in one male would suffice for many females. A possible view is that there is no use for the excess of semen, but that the stimulus for the hypertrophy of the sexual organs has been transmitted to the male from the female, where the necessity for the production of relatively large larvæ involves the hypertrophy of the organs. In this connection it may be mentioned that the eggs of the remarkable physogastric termitophilous dipteran, *Termitoxenia*, are likewise of considerable size.

DISPERSAL.—The means by which dispersal is effected in the case of the highly modified termitophilous creatures are altogether obscure. These termitophiles are sometimes so greatly specialised that they would be unable to live for any length of time outside the termite nest. The covering of cuticle is frequently very thin, and rapid desiccation occurs in a dry atmosphere.

On one occasion I observed a young *Paracorotoca* larva clinging to the side of the abdomen of a termite worker, and if workers sometimes enter a neighbouring nest in place of their own, it is possible for larvæ to be transported in this

way from one nest to another. It is conceivable that the larvæ attach themselves to the imagos of the termites issuing from the nest, and if such should be the case the beetle-larva would be associated with a pair of termites from the foundation of the colony. The only other supposition that seems possible is that occasionally under favourable atmospheric conditions, and probably at night, the adult beetles or larvæ wander out of the parent nest, and, meeting with foraging workers belonging to a neighbouring nest, return with them instead of with their former comrades. The adult beetle is very scarce, and it must often happen that only one individual is in a nest. Under such circumstances the sexual impulse would certainly induce a tendency to wander out of the nest.

These three suppositions would seem to exhaust the possible means of dispersal, provided the larval, pupal and imago stages are all undergone within the termite nest. Now, in the case of *Corotoca* it is stated by Schiödte that the larvæ are produced viviparously, and the extraordinary development of muscle which occurs around the oviduct of *Paracorotoca* supports the belief that this genus is also viviparous. Further, we have good evidence to regard the peculiar Staphylinid larvæ fairly commonly occurring in the nests of *Eutermes* as those of *Paracorotoca*. Also, Trägårdh found eggs in the oviduct of *Termitomimus*, which appeared to be on the point of issuing from the body, and, as already mentioned, it is extremely probable that the larva¹ has been found in a nest. Similarly in the case of *Termitomya*, certain insect eggs larger than those of the termites have been found in the nests inhabited by this dipteron, and Wasmann regards them as being its eggs. Thus the available evidence is entirely against the view that the larval stages of these termitophilous insects are passed outside the nest.

On the whole it is probable that the sexual impulse to

¹ An outline figure of this larva is given in my paper, "Termites and Termitophiles," Presidential Address, Section D, East London, 1919, 'South African Association for the Advancement of Science,' Report, vol. xvi, p. 99, pl. 9, fig. B, 1919.

wander in search of a mate is the main cause of the gradual dispersal of the species, and it may be added that the powerful pincer-like mandibles would certainly be of use as defensive organs in the dangerous expedient of wandering outside the nest.

BEHAVIOUR OF TERMITES TOWARDS PARACOROTOCÆ.—Whatever faults *Paracorotoca* may have as a guest—and the great size of the muscular jaws perhaps indicates an occasional meal of an immature termite—it is perfectly clear that its presence is not unwelcome to the host. I have never seen the worker or soldier termites exhibit the slightest attempt to attack either the larvæ or the adult beetles. In the confusion resulting from opening a nest I have sometimes seen workers attack each other, but the beetles are not interfered with.

The body of *Paracorotoca* bears certain characteristic swellings, and, as in other cases, it is not clear whether the blood-fluids ooze out through the thin cuticle of these outgrowths and are sucked up by the termites, or whether a volatile scent is exuded which is agreeable to the termites.

Among termitophilous creatures generally there is a marked tendency for the production of swellings from the body, serving as exudatory organs. These are very conspicuously seen in such different insects as the following: the termitophilous larva of a Tineid moth, described by Trägårdh; the larva¹ of a large dipteran, sent to me by Mr. Claude Fuller and at present undescribed; the adult *Paracorotoca* and *Spirachtha*; the supposed larva of *Paracorotoca*; the larva of *Termitomimus*, and in a lesser degree the adult. Thus these closely similar structures have arisen independently of one another in response to a similar need, i. e. the necessity for the guests to make themselves agreeable to their host.

DISTRIBUTION.—The largest number of adult beetles ever found in a single nest was five. This nest was a comparatively small one, measuring about 18 in. in diameter. On one occasion, in a nest measuring about 32 in. in diameter,

¹ In my paper already cited an outline figure of the larva is given.

a beetle was found in the superficial galleries after the first stroke of the trenching tool. The whole nest was rapidly removed in large pieces and transported in a tightly fitting box. Subsequently the material was carefully broken up on white paper in the laboratory and thoroughly examined, but not another beetle could be found, and I much doubt if any were overlooked. Although the adult beetle is scarce and excessively troublesome to find, the distribution is wide and does not appear to be in any way local. It is estimated that some 400 nests have been more or less carefully examined in this connection and the total number of imago beetles found amounts to 14. Commonly only one beetle is found in a nest. The supposed *Paracorotoca* larva is at least twenty times more plentiful. There is no clearly marked season, since both larvæ and adults have been found in summer and winter on all sides of Pietermaritzburg (altitude 2218 ft.) and also at Durban and Winkle Spruit on the Natal Coast.

From these facts it may be concluded that the species is scarce, but has a wide distribution; and if the West African species should prove to be the same it may be probably assumed that *akermani* occurs wherever *Eutermes trinerviiformis* is to be found.

II. SYSTEMATIC POSITION.

In a previous paper already cited it has been pointed out that the termitophile faunas of the various termite regions of the world have a striking external similarity, but systematically they do not appear to be more closely allied than the ordinary free-living faunas. If such termitophiles had been evolved before the general distribution of termites we might expect with some confidence, owing to the uniformity of the environment of termite nests, that a greater common element would exist throughout the termitophile faunas of the world. We must therefore suppose that after the main termite genera had arisen and become distributed the termite areas became geographically disconnected,

and the termitophiles were gradually derived from the free-living faunas of the different regions.

Where the present geographical connection is close, there we find greater affinity among the termitophiles: thus the *Æthiopian* and *Indo-Malay* termitophile faunas are definitely allied in that both possess such characteristic genera as the physogastric dipteron *Termitoxenia* and the Staphylinids *Termitodiscus* and *Corythoderus*.

Similarly, with regard to the extreme type of physogastrism, *Paracorotoca* is more closely allied systematically to the *Singapore* genus *Termitoptochus*¹ than to the *American* genus *Corotoca*, although in general aspect the *African* and *American* genera are extremely alike.

III. DEFINITION OF GENUS.

Paracorotoca gen. nov.

Head ovate, smooth, with shallow median convexity on frons; occiput with a shallow concavity on each side of the middle line. Compound eyes of medium size, somewhat large facettes. Antenna 11-jointed, first joint about $1\frac{1}{2}$ times the length of second. Mandibles edentulate, curved and pointed. First maxilla with a 2-jointed palp and a very large palpiger, the second joint tapering, terminal, and bearing a large olfactory pit on its anterior or dorsal surface. Second maxilla with ligula and palpigers fused to form a bilobed plate on which are inserted a pair of minute 1-jointed palps.

Pronotum smooth with median shallow concavity. Scutum quadrate. Elytra arched and supporting the overlying inverted abdomen. Alæ small, crumpled, membranous structures. Tibia elongated and cylindrical; tarsi 4-jointed; in the second and third legs the proximal tarsal joint is about twice as long as the 2nd.

Abdomen consists of ten segments with the first of the

¹ Silvestri, F., "Descrizione di un novo genere di Stafilinide termito-filo di Singapore," 'Boll. d. Lab. di Zoo. gen. e ag. in Portici,' vol. v, p. 37, 1910.

developed tergites, in segment II, and the first of the developed sternites in segment IV, first and second segments constricted to form a stalk carrying dorsally the inflated forwardly-directed portion. The up-bending of the abdomen occurs in the third segment. Abdominal sternites IV–VIII occur as five isolated transverse arches of considerable size. Abdominal tergites II–VI are present as narrow but strong transverse, chitinous bars, while tergites VII and VIII are wider and plate-like. Lower surface of inflated portion of abdomen concave and resting on the bridge-like elytra by two lateral longitudinal ridges.

Supposed exudatory structures are present as follows: two thin-walled backgrowths from the posterior surface of the metathorax, one lying on each side of the abdominal stalk; a bilobed swelling projecting medio-dorsally between the head and pronotum; and a median posteriorly directed swelling from the tergal region of abdominal segment VIII.

IV. DETAILED DESCRIPTION OF SPECIES.

1. EXTERNAL MORPHOLOGY.

Paracorotoca akermani (Warren).

Corotoca akermani Warren, Ann. Natal Museum, vol. iii, pt. 1, p. 105, 1914.

GENERAL FORM.—The head and thorax are essentially Aleocharine in character. The hind-wings or alæ are very rudimentary, being reduced to small crumpled, membranous structures concealed under the elytra. The anterior portion of the abdomen is constricted into a comparatively narrow, short stalk extending backwards in line with the head and thorax; the posterior portion is somewhat barrel-shaped and bears five separate, transversely-placed sterna; it is turned forwards towards the head with its morphological dorsal surface resting horizontally on the upper surface of the elytra. In the female the apex of the abdomen reaches forwards slightly in front of the middle of the pronotum,

while in the male, when the genital apparatus is not extruded, it does not reach beyond the hinder third of it (Pl. XVI, figs. 1-3).

If we accept Verhoeff's numbering of the segments of the abdomen of Coleoptera the up-bending appears to be in the 3rd segment.

DIMENSIONS.—The female is somewhat larger than the male and the abdomen tends to be more inflated.

(1) Total length (= distance from the nearly vertical surface of head to the hindmost end of the upturned abdomen), mean, 2.52 mm. in male and 2.98 mm. in female.

Largest male 2.95 mm., largest female 3.60 mm.

(2) Greatest vertical height of upturned abdomen, mean, 0.83 mm. in the male and 0.98 mm. in the female.

COLOUR.—The chitinous parts of the head and thorax are pale yellowish brown. The abdomen is translucent and whitish save for the sternites on the upper surface, which are yellowish, and the tergites on the lower surface, which are of a rich, yellow-brown. Tergites VII and VIII occur in the form of wide, shield-shaped, thin sheets of chitin and are pale yellow. In addition near the morphological posterior end of the abdomen there are two rounded indistinct pale yellowish areas on the dorso-lateral surface (Pl. XVI, fig. 3, *y. p.*).

HEAD.—Viewed from the front the downwardly directed head (fig. 4) is widely ovate, narrowing below. Labrum narrow, bilobed, setose; upper edge carries an internally projecting thickened ridge of chitin. Lower portion of clypeus membranous with an indistinct small spot (possibly a sense-organ) on each side; upper portion chitinised and slightly setose. Frons and vertex continuous, wide, slightly concave, almost glabrous, bearing antennal pits internal to the eyes close to anterior border. Pits have thickened edge indented below. At the junction of the frons and clypeus there is an internally projecting ridge continuous with the tentorium. Occiput with a concavity on each side and a narrow, median, posterior groove. Eyes of moderate size with

about 120 somewhat large facettes. Genæ convex, swollen, and extending round the back of the head, where they are separated from the labium by a thickened edge. Posterior foramen large, rounded (fig. 7).

Head-appendages: Antenna.—When stretched backwards the antennæ reach to about the middle of the metathorax. 11-jointed. The 1st or proximal joint about $1\frac{1}{2}$ times the length of the second, connected with antennal pit by inflated membrane, less setose than the more distal joints; joints 2–10 slightly tapering proximally, truncated distally, jointed to one another by narrow connections, richly setose; 11th or terminal joint fusiform, nearly double the length of preceding joint, provided with a ring of olfactory pits in the middle plane (Pl. XVII, fig. 20, *o. p.*). In some details this antenna is strikingly similar to that of *Termitomimus*.

Mandible.—Large, curved and pointed, without teeth or serration of any kind (Pl. XVII, fig. 21); the mandibles complete the lower contour of the head. Provided with very powerful muscles. Practically all physogastric Aleocharines have similar mandibles. At the base of the mandible and between it and the 1st maxilla there appears to be an aperture which would seem to be the only outlet for a gland lying close to the articulation of the mandible (Pl. XVI, figs. 5, 6, *d. m.*).

First Maxilla.—Cardo ring-like and narrow; stipes membranous towards the base; distally it carries a short, comb-like lacinia terminating in a curved, horizontally placed, finely pointed chitinous spur; galea membranous and curved, bearing a row of small reflexed setæ. The palpiger is setose, it is of great size and has the stipes attached to it on the inner surface. The palp is 2-jointed, although usually in these beetles it is 4-jointed (Pl. XVII, fig. 22). From comparison with other genera, as, for example, *Asticta*, it would appear that the 2-jointed condition arises through (1) the loss of the distal joint and (2) the proximal joint remaining incorporated with the palpiger. The second joint of the palp is curved and terminal, tapering to a blunt point. It bears on its anterior surface a large oval olfactory pit (fig. 23).

which is marked externally by a cluster of setæ. This maxillary palp differs considerably from that of *Termitomimus*, where there are 4 joints, and the last minute joint is placed terminally on a wide racket-shaped 3rd joint. On the other hand the 1st maxilla of *Paracorotoca* agrees in all essential points with that of the Singapore genus *Termitoptochus*.

Second Maxilla or Labium.—Submentum (cardo) more or less membranous and continuous with gular region; mentum (stipes) chitinous and provided with a few conspicuous setæ; distally there is a bilobed plate which may be regarded as being formed by the fusion of ligula on the anterior surface with palpigers on the posterior surface; the typical two pairs of lobes or paraglossæ (lacinia and galea) are not present. The labial palps on the posterior surface are remarkably reduced, they consist simply of two small tubercles bearing a small clump of long setæ. The edges of the bilobed plate bear a number of rows of short, scale-like setæ which produce a rasping surface (Pl. XVII, fig. 24). On the anterior face, which may be called the ligula surface, there is a curved row of short conspicuous setæ on each side. The labiums of *Termitoptochus* and *Termitomimus* are closely similar. The labium of *Corotoca* is less specialised, since from Schiödte's figure it may be judged that the palpigers and ligula are separable and the palps are 3-jointed.

Neck.—The neck is short. In the mid-dorsal line immediately in front of the pronotum the back of the neck or the front of the prothorax is produced into a translucent bilobed swelling. The lobes lie on the two slight concavities of the occiput of the head. The cuticle on the ventral surface of these lobes is roughened by the presence of minute tooth-like scales (Pl. XVII, figs. 30 and 31). This swelling would seem to be exudatory in nature, and any fluid actually diffusing through it would collect as a drop in the basin-like depressions of the occiput. An essentially similar structure is described by Trägårdh in *Termitomimus*, and Wasmann mentions the occurrence of an analogous swelling in the termitophilous *Scarabæid*, *Chætopisthes heimi* Wasm.

On each side of the floor of the neck there is a V-shaped sclerite with a very open angle facing outwards (Pl. XVII, fig. 25, *n. sc.*). The posterior limb of the V is short and thick and forms either a solid or hollow triangle. The anterior limb is of much greater length; it extends longitudinally, and the tip bears a little bunch of small bristles. Immediately in front of the end of the anterior limb there is situated a minute isolated sclerite.

THORAX.—The prothorax is distinctly marked off from the meso- and metathorax and considerable freedom of movement is here possible. The length of the prothorax is about $\frac{4}{11}$ of that of the whole thorax.

Prothorax.—The pronotum is a shield-shaped, convex plate (Pl. XVI, fig. 3). Dorsally there is a centrally placed shallow concavity with a length rather exceeding half the total length of pronotum. Laterally the pronotum bends downwards and has a somewhat thickened and inturned border. The border is slightly indentated by the socket for the articulation of the 1st thoracic leg. The pronotum is almost glabrous, but a few minute scattered bristles occur.

The sternal region of the prothorax is not strongly chitinised (fig. 2). The possible homologies of the chitinous pieces are now indicated (Pl. XVII, fig. 25). The narrow chitinous bar running transversely just in front of the coxal pits may be regarded as prosternum (*prs.*). On the inner side of the coxal pit there is a curved chitinous bar continuous with the prosternum; this is probably prosternal sternella (*p. st.*). Immediately surrounding the inner border of the coxal pit is a separate curved piece which may be the prosternal episternite (*p. ep.*); the outer border of the pit is formed by the indented thickened edge of pronotum (*pr.*). The coxal pits are open behind. On the posterior lateral surface of the prothorax there is a small crescent-shaped sclerite widely separated from the coxal pit; it may be prosternal epimeron (*pi.*). Immediately behind this sclerite there is a large spiracle which is conspicuously present in many Aleocharines.

Although a cuticle of considerable thickness is present the ventral surface of the prothorax behind the prosternum is white, soft and flexible, and may be transversely puckered in a complicated manner (Pl. XVII, fig. 34; Pl. XVIII, fig. 45).

Mesothorax.—The mesonotum is externally represented by the mesotergite or scutum, which is small, subquadrangular and yellowish-brown in colour (fig. 3, *sc.*), and the metatergite or scutellum, which is obscurely present behind. The mesosternum and mesosternal sternella appear to be represented by an area of chitinous plate in front of the coxal pits of the 2nd thoracic legs (fig. 2, *ms. st.*); it is continuous behind with the metasternal elements. Mesosternal episternite would appear to be represented by two curved chitinous bars in the coxal pit (fig. 2, *m. ep.*), while the mesosternal epimeron is not separately distinguishable.

Metathorax.—The line of origin of the alæ marks the front boundary of the metanotum. The acrotergite, protergite, mesotergite and metatergite may be supposed to be represented by the peculiarly shaped, thin sheets of chitin hidden under the elytra (fig. 3, *mt.*). The metasternum and metasternal sternella are fused with the mesothoracic elements to form a continuous ventral exoskeleton. The metasternal episternite (Pl. XVII, fig. 27, *mt. ep.*) is represented by a lateral elongated narrow plate attached to the metasternum; and the metasternal epimeron is not separately distinguishable, unless it is represented by a minute sclerite (fig. 2, *mi.*) in the coxal pit of the 3rd pair of legs.

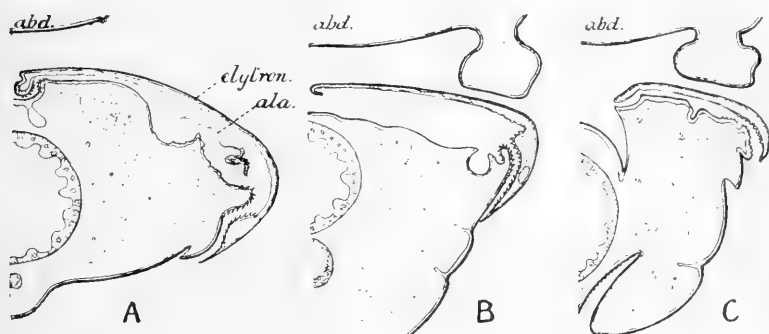
The metathoracic spiracle is placed rather far back between the metatergite and metasternal episternite (fig. 1).

Elytra.—The elytra are sub-rectangular convex structures (Pl. XVII, fig. 29) extending posteriorly a little beyond the metanotum. Short setæ are sparsely scattered on both surfaces. The elytra are well-adapted for supporting the heavy abdomen; the posterior edge is thickened on the inner surface and fits into a transverse groove on the dorsal surface of the body immediately behind the metanotum (Pl. XVIII, fig. 45). The outer edge of the elytron is sharply bent down-

wards, thickened, and provided on the inner surface with numerous scale-like setæ which catch on a roughened surface on the latero-dorsal edge of the metathorax (Pl. XVI, fig. 19). The relationship of the elytra to the abdomen and thorax is shown by a series of sketches in text-fig. 1, and it will be seen that the elytra constitute a supporting bridge which is not liable to slip, and distributes evenly the weight of the overlying abdomen.

Alæ.—The alæ are small, irregularly puckered, mem-

TEXT-FIG. 1.



Paracorotoca akermani. Diagrams showing the relationship of the elytra to the thorax and overlying abdomen. A. Transverse section through anterior region of metathorax. B. Through plane of metathoracic spiracle. C. Through anterior region of abdomen.

branous structures, in which there occur irregular pieces of chitinous tubes or ridges; these would appear to represent the broken-up venation of the wings (figs. 3 and 27). The alæ are quite functionless and are more abortive than in *Termitomimus*. They arise anteriorly at the junction of the metanotum and metasternal episternite.

Between the metasternal episternite and metanotum there is a membranous body-wall, and posteriorly this is expanded into a thin-walled backwardly directed pouch on each side. These lateral pouches lie alongside the abdominal stalk (fig. 2). A similar structure, but less conspicuously de-

veloped, was described by Trägårdh in *Termitomimus*. These outgrowths would appear to be undoubtedly associated with the termitophilous habit, and may be regarded as exudatory organs.

Legs.—The acetabulum of the prothoracic legs is open behind. There is no subcoxa, unless a portion of the skeletal edging of the acetabulum is to be so regarded. The coxa and femur are stout, subequal in length and bear short setæ. The tibia is nearly uniform in thickness throughout its length, it is much less stout than the femur and is slightly longer than it. The tarsus consists of 4 joints; the proximal joint is the longest, but the terminal joint, which bears two curved claws, is very nearly as long (figs. 25 and 26).

The acetabulum of the mesothoracic legs is less distinctly open behind (fig. 2). The coxa is of about the same length as that of the 1st leg, but the femur and tibia are considerably longer. The 4 tarsal joints are all longer, and the proximal joint is distinctly longer than any of the others (fig. 27).

The acetabulum of the metathoracic legs is very wide, and possibly the little isolated plate of chitin contained therein represents either a subcoxa or metasternal epimeron. The coxa is very short and wide. The femur and tibia are much longer than in the two first pairs of legs. The tibia is quite straight and nearly cylindrical. The first of the tarsal joints is by far the longest (fig. 28).

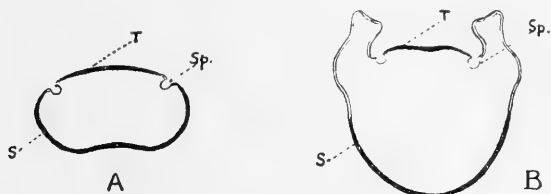
Leaving the coxa out of consideration the legs conspicuously increase in length from the 1st to the 3rd. In *Corotoca melantho* and *phylo* the tibia of the posterior leg is relatively much stouter and tends to be fusiform according to Schiödte.

ABDOMEN.—The most remarkable feature of *Paracorotoca* is the great inflation of the hinder portion of the abdomen. From the arrangement of the abdominal tergites and spiracles it would appear that Verhoeff's typical 10 abdominal segments can be recognised, and the inflation and up-bending begin in the 3rd segment. The 1st and 2nd segments are narrower

than the thorax and extend straight backwards in line with it (fig. 2).

The inflation of the abdomen involves the ventral and lateral surfaces and not the dorsal surface (text-fig. 2). The abdominal tergites are mostly narrow, transverse bars juxtaposed to the thorax. They are not wider from right to left than would be normal for a beetle of the size of *akermani*. On the other hand the upper, transverse, chitinous bands, really the abdominal sternites, are relatively much larger than would be normal for a beetle of the present size. Thus the inflation is not like that of a queen white-ant where

TEXT-FIG. 2.



Diagrams of transverse sections of the abdomen of typical beetle (A) and of *Paracorotoca* (B). *T.* Tergite. *S.* Sternite. *Sp.* Spiracle.

the tergites and sternites do not share in the enlargement of the abdomen, but remain as isolated structures on the greatly expanded intersegmental membrane.

Akermani is an active insect notwithstanding its relatively huge abdomen, and the movements of the insect must be greatly facilitated by the disposition of the parts of the body. On each side of the series of abdominal tergites there is a conspicuous longitudinal ridge (fig. 3), and these two ridges rest on a bridge formed by the two elytra, which are furrowed and roughened in such a manner as to fit on the surface of the thorax without slipping, and thus the bridge possesses a considerable stability and firmness (Pl. XVI, fig. 19, *El.*). By the upturning and forward extension of the abdomen the centre of gravity of the whole body comes to

lie somewhere over the legs, and mechanically this is more advantageous than dragging a heavy burden from behind.

Dorsal Surface.—Following Verhoeff's scheme it may be said that there is no tergite to abdominal segment I; but a pair of spiracles (1st abdominal) occurs at the anterior end of the stalk.

Abdominal segment II has a highly modified tergite. It consists of a median **X**-shaped sclerite bearing ventrally between the two arms on each side a very deeply-curved chitinous plate embracing both the abdominal stalk and the commencement of the upturned swollen portion of the abdomen (Pl. XVI, fig. 8). A spiracle (the 2nd abdominal) perforates the posterior portion of the arch.

Abdominal segments III, IV, V and VI bear relatively narrow tergites with a median ridge running from right to left, and with pairs of spiracles wedged between their extremities and the abdominal longitudinal ridges (fig. 3).

Abdominal segments VII and VIII bear plate-like tergites, and spiracles are absent. The chitin of tergite VIII is quite thin and even diffuse in character.

Abdominal segment IX is the last external segment; it carries a wide, curved, spatula-shaped tergite, and there is a conspicuous spiracle on each side (figs. 1 and 10, *sp.*).

Abdominal segment X is telescoped into segment IX; in the female it bears an obvious tergite which is richly provided with bristles; in the male this tergite would appear to be absent, unless two **U**-shaped chitinous structures at the base of the paramera or lateral lobes may be supposed to represent it. In both sexes sternite X is represented by a pair of setose plates.

In most insects there are 8 pairs of abdominal spiracles occurring in the first 8 abdominal segments, but in *Akermani* we find spiracles in abdominal segments I–VI and in IX. This presence of spiracles in the 9th abdominal segment is quite unusual, but in the present insect they are very obvious structures and are perfectly clear in section.

The less modified tergites, as those of segments III–VI,

have the appearance of being formed by the fusion of at least three elements, which doubtless may be regarded as the pro-, meso- and metatergites of a typical tergite.

The tergite of abdominal segment VII, although plate-like, also shows some signs of a compound nature; but the tergites of abdominal segments VIII and IX are simple plates. The thin tergite of abdominal segment VIII supports a forwardly directed swelling (Pl. XVII, fig. 33, and Pl. XVIII, *ab. sw.*), which is largely filled with blood-tissue. This swelling is probably a supplementary exudatory structure.

The position of abdominal spiracles III-VI at the ends of the tergites on the inside of the longitudinal ridges confirms the view that the inflation of the abdomen results from a ventral expansion, while the dorsal surface remains relatively unaffected.

Ventral Surface.—The abdominal stalk which joins the thorax consists of abdominal segments I and II. Each side is covered by a curved chitinous plate continuous with the tergite of abdominal segment II (fig. 2, *T.II*). The ventral surface of the stalk is not provided with special sternities; it is covered with a continuous, somewhat thick cuticle carrying long setae (Pl. XVIII). In one specimen an obvious transverse groove occurred in the middle of the ventral surface of the stalk, and this would seem to indicate the division between the 1st and 2nd abdominal segments; but such a groove could not be detected in all the specimens.

Expansion and up-bending occur in segment III. The ventral and posterior surface of this segment is richly setose. There is no development of a definite sternite in this segment.

Abdominal segments IV-VIII are provided with relatively large, arched sternites, each consisting of a narrow piece in front (topographical) and a much wider piece behind (Pl. XVI, figs. 1 and 9, also text-fig. 3); the former is metasternite (*mt. s.*), and the latter in section is seen to consist of a front portion or mesosternite (*ms. s.*) and of a hinder portion, presumably composed of pro- and acrosternites (*p. st.*).

The sternite of abdominal segment IX is a curved plate quite similar in character to the tergite below.

Abdominal segment X, telescoped into segment IX, bears a sternite consisting of a right and left setose plate. The two plates are close together on the upper surface in the female (fig. 14, *S.X.*), but in the male they are definitely lateral in position (figs. 11 and 12).

In the male the homologies of the chitinous structures of abdominal segment X are more obscure than in the female. The two trough-shaped lateral lobes together with the chitinous penis-tube can be everted far forwards. Associated with this apparatus the main chitinous parts are: (1) Two laterally placed setose plates, and (2) two U-shaped bars of chitin supporting and strengthening the lateral lobes or paramera (fig. 10, *T.X.*). From the relative position of these chitinous pieces it would seem probable that the former represent sternite X and the latter tergite X, but Trägårdh regards the latter as sternite in *Termitomimus*.

2. INTERNAL ANATOMY.

CUTICLE.—The cuticle tends to be of a more or less uniform thickness all over the body, but its density varies greatly. In the white or translucent portions of the body the cuticle is mostly as thick as elsewhere, but it is highly flexible and soft, and in certain places it is doubtless permeable to gases and probably even fluids. In most places the cuticle is seen to consist of two layers—an epistracum and an endostracum.

The external yellowish-brown areas which look like isolated plates of chitin in the whole specimen are, curiously enough, scarcely distinguishable in ordinary stained sections. The reason is this: the yellow chitinous plates (text-fig. 3, *pr. st.*, *ms. st.*, *mt. st.*) are quite continuous with the general cuticle (*g. cu.*) covering the body, and they are usually no thicker than the cuticle; they only differ from it in being denser and more homogeneous, and in being coloured bright yellow. In sections stained with orange the distinction between the plates and the surrounding cuticle becomes altogether obscure.

Thus the chitinous plates or sclerites of the body are hardened areas of the general cuticle. This hardening of the cuticle may involve both the epistracum (*epi.*) and endostracum (*end.*), as in the case of the head-capsule, and the two layers may then become quite indistinguishable and continuous; or it may involve only the endostracum, as in the case of the metasternite. Here the epistracum overlies the hardened endostracum, and is separated from it by a narrow space (text-fig. 3, *mt. st.*).

To some extent the general cuticle varies in thickness in different parts of the body, and generally the thicker the cuticle the greater the vertical height of the hypodermal

TEXT-FIG. 3.



Paracorotoca akermani. Longitudinal section through ventral exoskeleton of one abdominal segment.

epithelium. The cuticle has been examined carefully with Zeiss Ap. 1.5 mm. and H. Imm., and it may be definitely affirmed that there is no general system of minute canals perforating it. The endostracum stains to some extent with hæmatoxylin, and this is also the case with the epistracum in certain parts of the body. It is thought that the staining capacity of the cuticle is associated with a certain looseness in texture which will permit the passage of gases and even fluids, although no actual pores may be visible. The only place where there appeared any definite signs of a canaliculation of the exoskeleton was in the sternal region of the metathorax in front of the acetabulum of the third pair of legs (Pl. XVII, fig. 35, *end.*). Here a distinct vertical or oblique striation could be seen in the sections. This striation seemed to be caused by the presence of very numerous minute cracks or canals which, however, did not appear to reach the

surface of the chitin and form actual pores. Even if definite pores are not present, the existence of the cracks or canals would materially assist in the slow filtration of fluids or gases through the somewhat thick chitin. The lack of a clearly-marked porosity is doubtless associated with the ever-present danger of desiccation.

It is instructive to note the places in the body where the chitin was found to be especially stainable with hæmatoxylin. These were, in descending order of staining intensity: (1) A complicated frill on the ventral surface of the prothorax (Pl. XVIII, and XVII, fig. 34); here the epistracum and endostracum tended to be remarkably separated from each other, and the relatively thick hypodermis was separated from the endostracum by a granular stainable substance. (2) The dorsal anterior bilobed swelling of the prothorax, overhanging the back of the head; the terminal portion stained more especially (fig. 30). (3) The backwardly directed swellings of the metathorax (fig. 32). (4) The ventral surface of the abdominal stalk and the lower surface of the swollen abdominal segment III. These various places are favourably situated as regards accessibility to the termites, and it is probable that substances derived from the blood-tissue exude over these areas.

Around the base of the larger setæ there may be a circular crack leading into the space between the general cuticle and hypodermis (Pl. XVII, fig. 38). Doubtless the body-fluids can exude through these perforations.

THE HYPODERMIS.—The hypodermis or epidermis varies greatly in thickness in different parts of the body. It is usually one cell thick, and consequently the varying thickness depends on the depth of the individual cells. Under the abdominal sternites the hypodermis may be more than one cell thick (Pl. XVI, fig. 9). In some parts of the body the hypodermis is withdrawn away from the cuticle more or less considerably, and the resulting space contains a coagulated substance readily stainable with hæmatoxylin (Pl. XVII, fig. 32, *cg. m.*). According to Trägårdh it is this substance

which exudes from the body for the delectation of the termites.

Hypodermal Glands.—The following paired glands are present: (1) mandibular, (2) cephalic, (3) tergal scent-glands of abdominal segment VI, (4) sternal glands of abdominal segment X, developed in the female, absent in male. No trace of prothoracic glands such as those described by Trägårdh in *Termitomimus* could be found.

The mandibular glands consist of a conspicuous mass of large glandular hypodermal cells at the base of the mandible and 1st maxilla of each side. The gland appears to discharge its secretion through a soft spot on the cuticle lying immediately between the bases of these appendages (Pl. XIX, fig. 57, *d. m.*). The nuclei of the glandular cells are particularly large, and the absence of cell-outlines seems to be characteristic. Very possibly these glands secrete a saliva-like fluid which may be taken up by the termites in exchange for their own saliva.

The cephalic glands are two dorso-lateral patches of hypodermis consisting of tall, glandular cells which appear to open by pores in the cuticle of the occiput immediately under the overhanging pair of prothoracic swellings (Pl. XVIII; and Pl. XVII, fig. 36, *gl. ep.*).

The two tergal glands of abdominal segment VI consist of a cluster of large, much swollen hypodermal cells which discharge their secretion into well-defined, chitin-lined receptacles provided with a duct. They are so placed as to be entirely inaccessible to the termites, and as they are similar in character to organs regarded as scent-glands in other insects, we may reasonably assume that they produce a scent agreeable to the termites. The secretion which is passed into the receptacle is capable of coagulation and staining (Pl. XVI, fig. 19, *g. r.*, and Pl. XVII, fig. 37, *R.*).

The sternal gland of abdominal segment X is probably also a scent-gland, but since it is not present in the male we may assume that it has a sexual function, and possibly it is of use for sexual recognition. The glands consist of a pair of

clusters of large, swollen hypodermal cells; these discharge into two chitin-lined oval recesses lying between segment IX and the telescoped sternum of segment X. The secretion in the recesses coagulates and stains very intensely with hæmatoxylin (Pl. XX, figs. 79 and 80, *gl. c.*).

Trichogenic Cells.—Wasmann lays stress on glandular bristles in termitophilous insects. In a typical glandular bristle the trichogenic cell produces the bristle, and around this cell are one or more glandular cells which pour their secretion into the hollow bristle or at the base of the bristle where it perforates the general cuticle. In *Termitomimus*, Trägårdh figures and describes enormous trichogenic cells passing up into exceedingly minute bristles; the cells and bristles are entirely disproportionate to each other, and he suggests that these cells may have a secretory function in addition to that of producing the bristle itself.

In *Paracoratoca* the trichogenic cells are not very considerably larger than the ordinary hypodermal cells (Pl. XVII, fig. 38, *tri. c.*). They contain a globular vacuole and are in direct continuity with the swollen base of the bristle. These trichogenic cells are certainly not actively secreting cells pouring a fluid on the surface of the cuticle; they have produced the bristle, and their main function has been accomplished.

As in the case of *Termitomimus*, the hypodermis in some parts of the body is withdrawn from the cuticle, and in the space there occurs a fluid which is coagulated and granular in the preserved specimen, and this substance stains readily. It would appear that the blood-tissue diffuses through the hypodermis and is thereby altered, and the resulting fluid accumulates between the hypodermis and the cuticle. This fluid presumably passes in some way through the cuticle either in vapour or as a liquid. We have seen that certain kinds of cuticle are probably permeable to this fluid, and where bristles occur there would seem to be ready means of egress around the bases (fig. 38).

TRACHEAL SYSTEM.—No elaborate investigation on the

distribution of the tracheal tubes has been made. The arrangement of the spiracles has already been indicated. There is a large spiracle immediately behind the prosternal epimeron and generally regarded as prothoracic. No clearly defined mesothoracic spiracle could be found, but a metathoracic one (Pl. XVI, fig. 1) is present, being placed rather posteriorly and latero-dorsally. Abdominal spiracles, not sensibly smaller than the thoracic ones, occur associated with segments I-VI and IX (figs. 3, 10); these are all placed dorsally, and except the last are completely hidden from view in the normal position of the abdomen. The first abdominal spiracle occurs at the commencement of the abdominal stalk, the second perforates the modified tergite of abdominal segment II, while the 3rd-6th spiracles lie between the tergites and the longitudinal ridges. The absence of spiracles to segments VII and VIII is doubtless associated with the modification of the tergites in connection with the support of the great colon and the median abdominal exudatory organ. The development of a spiracle associated with segment IX is unusual; perhaps it is formed in compensation for the loss of spiracles in the two preceding segments.

All the spiracles of the body are similar in structure. The spiracular chamber is pear-shaped and bears a large circular external opening, the internal aperture of the chamber is minute, and there is a small occluding apparatus (Pl. XVII, fig. 38A, *o. m.*). There are no bristles of any kind guarding the external aperture.

It may be mentioned here that there is an especially large tracheal vessel in connection with the tritocerebrum (Pl. XIX, figs. 46 and 56).

THE FAT-BODY AND BLOOD-TISSUE.—Although there is a considerable amount of fat-body, yet it cannot be regarded as very greatly hypertrophied or excessively abundant. In the male the inflation of the abdomen is chiefly due to the large size of the mesenteron and the hypertrophy of the male generative organs. In the thorax, short cords of large-sized fat-cells are irregularly scattered and surrounded by coagulated

blood. In the inverted abdomen the fat-cells form a more compact tissue running on each side, especially just above and in the two longitudinal ridges which rest on the elytra (Pl. XVI, fig. 19, *ab. r.*). There appears to be but little coagulated blood in this portion of the body. Towards the anal end of the abdomen there is a continuous, thin layer of blood lying immediately under the hypodermis of the dorsal surface. In section it is seen that the median prothoracic dilatation, the backgrowths of the metathorax and the median swelling supported by tergum VIII are filled with coagulated blood, but there may be an irregular strand of fat-tissue towards the middle of the cavities (Pl. XVII, figs. 32 and 33). There is a certain amount of fat-tissue in the metathoracic dorsal region (Pl. XX, fig. 74), and there is a fairly thick and continuous sheet nearly filling the space between the huge mesenteron and the hypodermis of the abdomen (Pl. XVIII, and Pl. XIX, fig. 59, *f. b.*)

Similarly in the female there is no excessive amount of fat-body. The physogastrism is mainly due to the great bulk of the genital organs and of the mid-gut.

There is relatively more fat-tissue in *Termitomimus*, but nevertheless Trägårdh seems to under-estimate the effect of the hypertrophy of the sexual organs in connection with the physogastrism of this beetle.

Trägårdh states that in *Termitomimus*, where the cuticle is thin and an endostracum is absent, there the hypodermis may be very tenuous or scarcely discernible and is pressed close to the cuticle by the underlying fat body. On the other hand, where the cuticle is thick and an endostracum is present there the hypodermis is thick and tends to be withdrawn from the cuticle.

In *Paracorotoca* there is no doubt that the thickness of cuticle and the depth of the hypodermis tend to vary *pari passu*, but the withdrawal of the hypodermis from the cuticle and an accumulation of coagulable substance would seem to depend primarily on the absence of pressure of the internal organs and not on the presence or absence of underlying

fat-body. Where there is considerable pressure there the hypodermis is mostly thin and the cuticle is also thin. It may be readily understood that a thin, stretched hypodermis would only be capable of secreting a thin cuticle. It is clear that the varying thickness of the general cuticle depends partly on this effect of internal pressure.

HEART.—The heart proper lying within a pericardium is exceptionally short; it appears to be confined to segments VI and VII in the reflexed abdomen. Anteriorly the heart is continued into a uniform dorsal aorta which bends on itself and runs forward immediately above the œsophagus as far as the procerebral lobes (Pl. XVIII, *H*). The restriction of the heart proper to the reflexed portion of the abdomen is doubtless associated with the sharp bend contracting the dorsal surface of the anterior abdominal segments and the pressure exerted by the hypertrophied organs.

In *Termitomimus* the heart proper is even shorter than in *Paracorotoca*; it appears to be confined almost entirely to segment VI and a portion of VII; both anteriorly and posteriorly it communicates with a well-defined narrow aorta.

MUSCLES.—The musculature has not been especially investigated, but the most characteristic feature is the extraordinary development of muscle around the convoluted vagina. These muscle-fibres are mainly transverse and form a very strong investment. It is extremely probable that this great muscular development is associated with the birth of relatively large viviparous young (Pl. XVIII, fig. 45, *m. s.*; Pl. XX, fig. 78, *m.*). The muscular systems of the ejaculatory duct and of the sucking pharynx are also much developed.

GENITAL ORGANS.—Male.—These organs are greatly hypertrophied. There are two large testes; the left is pushed in front of the right, and they occupy a large portion of the cavity of the inflated abdomen. Each testis consists of a number of large follicles which dehisce inwardly into wide channels opening into a central cavity (Pl. XVI, fig. 19; Pl. XX, fig. 73, *s. ch.*). From the central cavity of each testis there arises a narrow, short vas deferens (Pl. XIX, fig. 63, *s. d.*).

The two vasa deferentia open close together at the front end of the muscular ejaculatory duct. Opening out of each vas deferens close to its junction with the ejaculatory duct there is a capacious, lobed vesicula seminalis (*v. s.*) in which a large quantity of semen can be stored. Dorsally there occur the accessory glands (*ac. g.*) which consist of two blind tubes with glandular walls; these open into the vasa deferentia close to the openings of the vesiculæ seminales.

The ejaculatory duct enters, on the ventral (upper) side, a very long, curved, chitinous penis-tube (*ch. p.*) which is inflated at the inner end. The external aperture for the virgal tube is bounded by slight chitinous knobs and is subterminal, as is normally the case (Pl. XVI, fig. 10, *ch. p.*). The chitinous penis projects dorsally (i.e. turned towards the lower surface of the reflexed abdomen). Obliquely situated, one on each side of the chitinous penis, are the lateral lobes or paramera (*l. l. l.*; *r. l. l.*). These are strengthened by chitinous plates of various shapes and sizes. The largest sclerites are U-shaped; there is one at the base of each lateral lobe, and it is possible that they represent tergite X (*T.X.*).

Two follicles of the testis are shown in Pl. XX, fig. 73. The flat epithelium lining the seminal chamber (*s. ch.*) is greatly modified opposite to each follicle. The epithelium becomes more than one cell thick; the individual cells are perforated and are loosely arranged leaving intercellular spaces. Through this porous or reticular tissue the ripe spermatozoa (*spz.*) pass singly into the seminal chamber. The tissue acts as an efficient sieve, and prevents the clusters of spermatocytes and wisps of spermatozoa from passing out of the follicle.

The vesiculæ seminales are richly branched; the wall consists of very flat cells in which the nuclei have almost completely disappeared (Pl. XIX, fig. 65). These cells would seem to form a purely inert epithelium which is almost cuticular in nature. An exceptionally large quantity of semen is stored in these vesiculæ seminales.

The accessory gland has a thin outer muscular coat. The

epithelium consists of exceedingly tall and slender cells, and the inner portion of these appears to be gradually transformed into a thick secretion which fills the lumen of the gland (Pl. XIX, fig. 64, *s. ep.*).

The external male organs are shown semi-diagrammatically in side view in Pl. XIX, fig. 68. Here the organs are partially extruded. The chitinous penis or middle lobe (*ch. p.*) is seen within a sheath (*sh.*) lined by a thin cuticle continuous with the general exoskeleton. The lateral lobes have become shifted in position, doubtless in association with the inverted position of the abdomen; the right lateral lobe (*r. l. l.*) is almost ventral (uppermost) and the left lateral lobe (*l. l. l.*) is nearly dorsal (figs. 66 and 67).

When fully everted there is a ring-like swelling around the base of the lateral lobes; this is doubtless the "basal-piece" of Sharp and Muir¹ (Pl. XVI, figs. 11 and 12, *b. p.*). In front of this, the soft integument of the abdomen bears a pair of setose plates which we have already regarded as representing sternite X, while tergite X is perhaps modified into the U-shaped gonapophyses at the base of the lateral lobes.

In the mid-ventral line there is a conspicuous internal chitinous rod (Pl. XIX, fig. 68, *m. ch. r.*), which is an ingrowth from the ventral recess of the genital vestibule. To this, important muscles associated with the lateral lobes are attached. The ejaculatory duct is very narrow and very muscular. It enters the chitinous penis by a foramen situated near the posterior end on the morphological ventral surface (fig. 68). The ejaculatory duct runs through the relatively wide chitinous penis, and near its apex it widens into a small "internal sac" (Sharp) (*i. s.*) which is somewhat crumpled, but by the action of certain muscle and probably also by fluid-pressure the sac can be everted (Pl. XVI, fig. 10, *i. s.*). This internal sac is singularly small, and its reduced size and soft condition are doubtless connected with the fact that there is no definite bursa copulatrix in the female apparatus.

¹ Sharp, David, and F. Muir, "Anatomy of the Male Genital Tube of Coleoptera," 'Trans. Ent. Soc. Lond.,' 1912-13, p. 481.



In Pl. XIX, figs. 69-72, a series of transverse sections, cut from behind forwards, is given, showing the relationship of the chitinous tube to its sheath. Internally the chitinous tube is lined by hypodermis continuous round the edge of the foramen with the general hypodermis of the sheath (fig. 70, *e. c.*), which, owing to the development of muscle, is greatly interrupted. In fig. 71 the entrance of the ejaculatory duct through the foramen is shown. The wall of the sheath is highly muscular, consisting largely of longitudinally arranged fibres. At the anterior end of the chitinous penis there is a thick mass of muscle, and just in front of the plane passing through the maximum diameter of the swelling of the tube there are some well-marked oblique and transverse bands of muscle (fig. 70, *t. m.*). By the contraction of these various systems of muscles the genital apparatus is squeezed out during copulation.

Female.—The vagina is a long convoluted tube extending forwards ventrally to abdominal segment VI. Internally it is lined by cuticle, while on the outside there is an exceptionally powerful sheath of muscle-fibres. Anteriorly the vagina receives two thin-walled oviducts; the left extends forwards, while the right one appears to be branched, one limb extending forwards and the other backwards (Pl. XX, fig. 75). These thin-walled oviducts bear a number of very short ovarian tubes, consisting of one or two pairs of elements. There seem to be six tubes associated with each oviduct, but it was not possible with the available material to be certain with regard to the number. A pair of elements consists of a distal mass of nutritive cells and a proximal ovum (figs. 76 and 77). The ovarian tubes are in very different stages of development at any one time. The eggs grow to a great size; at first, when the egg is small or of medium size, the protoplasm is granular and does not carry yolk-globules, but later a dense mass of large globules is produced. The nucleus of the egg becomes distinctly stellate. As the egg matures the nutritive tissue dwindles, and ultimately it forms a little mass of cells attached to the distal end. It is probable that

development occurs in situ while the egg lies in its ovarian tube. Afterwards it is to be supposed that the larva passes down the oviduct into the muscular vagina and is then squeezed out to the exterior. When the ripe ovum or young larva has been passed out of the ovarian tube the old egg-follicle and nutritive tissue would seem to undergo a curious transformation into a kind of corpus luteum. The cells shrink and the nuclei become very irregular and stain deeply (fig. 76, *c. l.*).

The posterior end of the vagina is eversible as a very short ovipositor (Pl. XVI, fig. 15, *f. d.*). This structure is bounded on each side by two short lobes constituting a kind of sheath comparable to the lateral lobes of the male (*r. l. l.* and *l. l. l.*). A transverse section of the vagina close to the external opening and showing the folded nature of the wall and the muscular coat is given in Pl. XX, fig. 78.

The posterior end of the vagina is provided with a pair of large clusters of glandular cells forming accessory sexual glands (Pl. XX, fig. 75, *gl. c.*). As already described, the cells of a portion of these glands discharge into the ventral recess between sternites IX and X (fig. 79).

The secretion (*sec.*) of the gland is seen both in the recess and in the lumen of the vagina (fig. 80). Possibly it is odoriferous and serves for sexual recognition. A similar gland is not found in the male.

There is no clearly defined bursa copulatrix.

The spermatheca is a somewhat elongated curved tube (Pl. XX, fig. 75, *spt.*), and is situated rather far forward in the 8th abdominal segment (Pl. XVIII). It arises in connection with a large bilobed spermathecal gland, placed on the right side of the body, and runs to the middle line dorsal to the vagina and ventral to (above) the colon. The spermatheca is lined by a cuticle which is very conspicuously striated like a trachea. Although very carefully looked for in three series of sections, a spermathecal duct (indicated by dotted lines in fig. 75) from the vagina could not be discovered. In all three cases the spermatheca was filled with semen, and

it is therefore conjectured that perhaps after copulation the duct disappears and fertilisation is effected not viâ the vagina and oviduct but by direct passage from the spermatheca through the hæmocœl to the ripe ova in the ovarian tubes.

The cells of the spermathecal gland are of great size with large nuclei and fairly well-defined cell-outlines (Pl. XX, fig. 81). These cells bear large vacuoles filled with a somewhat dense secretion, which is discharged in the middle of the gland into an irregular canal (*gl. d.*) communicating with the spermatheca. It is to be supposed that the secretion of the gland preserves the vitality of the stored semen, and it may assist in the discharge of the semen (*se.*) from the spermatheca (*s. w.*). In this connection the muscles (*m.*) surrounding the spermathecal-wall will play an important part.

In *Termitomimus* the female genital organs are essentially similar, but they are rather simpler in character. The median vagina consisting of a high epithelium and surrounded by a muscle-layer runs forwards ventrally and opens directly into a somewhat dilated sac with thinner epithelium. This sac is slightly bilobed in front, and is expanded laterally. The lateral wall of each side bears about six short ovarian tubes, consisting, as far as observed, of a single pair of elements, a distal mass of nutritive cells and a proximal ovum surrounded by a layer of follicle cells. This anterior sac presumably represents the fused right and left oviducts. The spermatheca is more globular than in *Paracorotoca*, but there is a quite similar, large, bilobed spermathecal gland associated with it.

ALIMENTARY CANAL.—The gut exhibits considerable reduction and specialisation. It may be divided into: (1) stomodæum, consisting of (a) mouth and pharynx, (b) pumping apparatus or sucking pharynx and (c) long, gradually widening œsophagus; (2) mesenteron; (3) proctodæum consisting of (a) ileum, (b) colon and (c) rectum (Pl. XVIII).

Mouth and Pharynx.—The mouth is very small; it is bounded above by a chitinous setose labrum and below by a

somewhat extended, trough-like labium. The pharynx is a vertical, narrow tube with a relatively thick, cuticle layer continuous with the exoskeleton. The lumen of the pharynx is circular in cross-section, and no distinct hypopharynx or clearly-defined epipharynx are developed. At some little distance up the pharynx there is a slight ridge on each side bearing short setæ. Possibly these are gustatory in character, and the two ridges may represent the remnant of an epipharynx (Pl. XVII, fig. 24A, *g. ri.*). The inner surface of the labium is provided with numerous close-set short setæ (fig. 24A).

Although carefully searched for no typical salivary glands opening into the gut could be found.

Sucking Pharynx.—The vertical, narrow pharynx opens into a dilatation in the middle of the head. This is provided with a well-developed system of muscles consisting of strong, striated muscle-fibres. The musculature comprises longitudinal fibres in contact with the sac and clumps of radial fibres extending to the wall of the head-capsule and internal skeleton. There appear to be six more or less distinct clumps: a fronto-dorsal, a fronto-ventral, a pair of dorsal and a pair of lateral. This muscular system is strikingly similar to that of the sucking pharynx of a butterfly, and here we have a convergence of structure probably arising through the circumstance that the methods of solving the mechanical problem are necessarily limited by the organisation of the head of an insect. The sucking pharynx is lined by a cuticle continuous with that of the narrow pharynx. From Trägårdh's description it is clear that the muscles of the pharynx in *Termitomimus* are closely similar.

Œsophagus.—From the posterior wall of the sucking pharynx the œsophagus arises as an exceedingly narrow tube which is closely surrounded by the cephalic nervous system. On passing into the thorax it gradually dilates until it opens into the mesenteron in the hinder region of the metathorax. There is no suggestion of a crop and no gizzard nor pro-ventriculus. The œsophageal wall is provided with a well-developed muscle layer (Pl. XIX, fig. 58, *m. c.*), a very thin

layer of connective tissue and a somewhat peculiar ectodermal epithelium. Anteriorly the cuticle lining is more or less smooth (Pl. XVIII) and resembles that of the sucking pharynx; posteriorly the cuticle is thick and almost fibrous in character, it is not sharply delimited from the epithelium itself, and it is raised into prominent, pointed spines (*spi.*). These spines are very long and numerous and extend over the posterior two-thirds of the œsophagus; they must constitute not only a very efficient strainer, but must serve to commingle the food mass as it is forced through it.

The œsophageal epithelium is invaginated into the front end of the mesenteron to form a small but quite definite œsophageal valve consisting of tall cells. This invagination involves the thin connective tissue but not the muscle-layer of the gut-wall. The valve forms an obvious constriction between the œsophagus and mesenteron and doubtless the passage can be entirely closed in this plane (Pl. XVIII, *w. v.*).

Mesenteron.—This portion of the gut in *Paracorotoca* is very large, not to say hypertrophied (Pl. XVIII). It extends from the metathorax to the region of abdominal segment VII. In the ordinary position of the abdomen the main portion is V-shaped with the two limbs approximately equal. At the posterior end (morphological) the mesenteron is sharply bent on itself dorsally, it narrows greatly and joins the ileum of the proctodæum in the region of segment VI. The endodermal epithelium of the mesenteron consists of cells of very irregular height giving a conspicuously waved inner surface (Pl. XIX, fig. 59, *e.*). Many of the cells possess large clear oval vacuoles of the usual type. In transverse section the wall of the mesenteron may show considerable longitudinal folding (fig. 60). Wedged at the base of the columnar cells there are small deeply-staining cells (*gl. c.*) resembling the cells which secrete HCl in the gastric gland of a mammal. It appears that the vacuolated cells are sometimes bodily discharged into the food-mass, since a number were found embedded in it in a good series of sections. On

the inner surface of the epithelium a peculiar, thin, continuous layer of substance (*l. sc.*) was observed. The layer carried clusters of black granules. The nature of the layer is obscure; it may be coagulated digested food which was being absorbed by the columnar epithelium.

A characteristic feature of the mesenteron of *Paracorotoca* is the complete absence of caecal tubes. In *Termitomimus*, as pointed out by Trägårdh, the mesenteron gives off a few, very short, thick diverticula which doubtless represent reduced caecal glands, but in *Paracorotoca* there is no sign whatever of such outgrowths.

Proctodæum: Ileum.—It is short and narrow and runs obliquely forwards to join the expanded dorsally placed colon (Pl. XVIII, *il.*). There is an outer muscular coat (Pl. XIX, fig. 61, *m.*). The ectodermal epithelium consists of cells of very irregular height with large nuclei (*ec.*). No well-defined cuticle was visible. In transverse section some 5–8 prominent longitudinal ridges of epithelium can be seen projecting into the lumen.

With the material available it was not easy to ascertain with absolute certainty the number of Malpighian tubules, but in three series of sections only a right and left tubule could be seen joining the ileum dorsally at its junction with the narrow end of the mesenteron (Pl. XVIII, *e. m. t.*). The diameter of the portion of the tubules connected with the gut was very small, and less than half that of the convoluted tubules cut through in the abdomen and posterior part of the thorax. Doubtless the proximal portion of the tubule as it approaches the gut is not excretory, but acts simply as a duct, since the cells forming it are not large and swollen like those of the convoluted and more distal portion of the tubule. The number of Malpighian tubules given for *Staphylinids* is 4, and 6 in the larva; while in *Paracorotoca* I could only detect 2 in the imago and 4 in the supposed larva.

In *Termitomimus* there appear to be 4 Malpighian tubes, two on the right and two on the left, opening into the dorsal wall of the extreme anterior end of the proctodæum. The

proximal portion of the tubes near to the entrance to the gut is less swollen than the distal part, but the distinction is not so strongly marked as in *Paracorotoca*.

Colon.—The colon is expanded greatly and extends through the greater part of segments VI–VIII. In the case of two female specimens sectioned the colon was situated dorsally on the left side of the middle line. The ileum was bent ventrally and ran backwards to join the mesenteron ventral to the colon (Pl. XVIII, fig. 45, *il.*). In the single male specimen examined the colon was more ventral, and the ileum joined the mesenteron dorsal to it (Pl. XVI, fig. 19, *mes. il.*). Whether this is a sexual peculiarity or a mere individual variation in the arrangement of the parts could not be determined with the limited material.

The colon has a pronounced muscular coat (Pl. XIX, fig. 62). The ectodermal epithelium (*p. ec.*) consists of small, very irregularly shaped cells which are inert in character, and more or less cuticularised as a whole, and not merely covered by a thin layer of chitin.

Rectum.—The rectum is short and narrow; it leads to the anus which is situated immediately dorsal to the genital aperture (Pl. XVIII, *r.*). The ectodermal epithelium consists of short, fairly regularly arranged cells, and the cuticular lining is more obvious than in the other portions of the proctodæum.

Food.—Discrete masses of solid food were never found in the gut. It was always filled with an eosinophilous granular substance. In the œsophagus the substance was coarsely granular and very highly eosinophilous, in the mesenteron it was finely granular, uniform in texture and less highly eosinophilous, while in the colon it was very finely granular and scarcely stainable. From the nature of the sucking pharynx and from the extreme tenuity of the anterior portion of the œsophagus we may conclude that the food is entirely of a fluid nature.

NERVOUS SYSTEM.—The central nervous system exhibits considerable modification with reference to the absence of a

series of separate abdominal ganglia. On the other hand, the presence of a definitely double nerve-cord in the thorax is a primitive character.

The cephalic region of the nervous system was studied by means of a model made by glueing together a series of cards cut to shape from camera lucida drawings of serial sections of a male beetle.

The protocerebrum consists of a pair of procerebral lobes, which in dorsal aspect are pear-shaped, and of a pair of optic ganglia which are situated far forward at the anterior ends of the procerebral lobes (Pl. XIX, fig. 46, *proc.*, *op. g.*).

The deutocerebrum consists of the antennary lobes; they are attached to the anterior surface of the procerebral lobes immediately below the optic ganglia (fig. 47, *a. l.*).

Ventrally the procerebral lobes are in wide connection with a large subœsophageal ganglionic mass (fig. 47) extending backwards as far as the plane of the prosternum (Pl. XVIII).

The tritocerebrum is present as a small rounded lobe placed behind the procerebral lobes, one on each side of the œsophagus (fig. 47, *tri.*). A large trachea is associated with it.

A ventral view of the cephalic system is seen in fig. 48. The subœsophageal ganglion (*sub. g.*) is deeply indented in front, and the roots of the mandibular (*md.*), maxillary (*m. n.*) and labial (*l. n.*) nerves are indicated.

The general distribution of cortex and medulla has been traced in a series of sections; but abundance of material and elaborate technique would be necessary for obtaining a full knowledge of the course of the various tracts.

The optic ganglion is comparatively small, and in vertical transverse section (figs. 49, 50, 51) it was seen that some of the cells of the cortex are modified and perhaps degenerate in character (*d. c.*, *d. n. c.*) The nuclei are very small and perfectly homogeneous. No cell-outlines were visible. It will be seen that these small, deeply staining nuclei are clustered around a small mass of medulla. The nuclei are much smaller than, and have not the same structure as, those clustered in the calyx of the procerebral lobes. Quite possibly this modifica-

tion of some of the cells of the cortex is associated with the degenerate character of the compound eyes.

In fig. 50 a portion of the antennary lobe (*a. l.*) is shown springing from the ventral surface of the optic ganglion (*d. c.*). The antennary lobe gives off a stout nerve to the antenna (fig. 46, *a. n.*).

The canal for the œsophagus, which passes through the cephalic nervous system, is very narrow in front (fig. 53), but it widens out considerably behind (fig. 55).

The procerebral lobes are not richly provided with cortex in comparison with many other insects. The great bulk of the lobe consists of medulla, as is seen in fig. 53. The nerve-tissue is bounded on the outside by a thin, flat epithelium (fig. 54, *ep. c.*), consisting of cells which exhibit a considerable density, and are quite unlike the ordinary cells of the cortex. The epithelium can be traced with more or less clearness over the whole of the nerve-cord. A similar epithelium, but not so sharply defined, was observed in both *Termitomimus* and *Termitodiscus*. It would appear that the epithelium is not nervous in nature, and very possibly it is to be regarded as a layer of less differentiated ectoderm; but for any certainty in the matter a study of the development is necessary. The cortex is exceedingly thin and sparse on the lobes (fig. 53) until we reach quite close to the posterior vertical periphery (i. e. at a plane just in front of the tritocerebrum, *tri.*, fig. 46); here the cortex thickens to some extent, and we find a weakly developed mushroom-body consisting of a small calyx (fig. 54, *cy.*) with a stalk or cauliculus (*ca.*). On the calyx rests a small trabecula (*trb.*). The nuclei of the trabecula are smaller than those of the rest of the cortex, and no cell-outlines are discernible. The tissue of the trabecula stains more deeply than the rest of the cortex. At fig. 55 the section passes very close to the vertical face and the calyx (*cy.*) and calyx-cells (*cy. c.*) are disappearing. The relatively small amount of cortex which is present is clearly shown in the vertical, longitudinal section given in Pl. XVII, fig. 43.

There occurs a bridge of transverse fibres connecting the

two procerebral lobes, and it is equivalent to the "central body" of same authors (Pl. XIX, fig. 54, *b.*).

The tritocerebrum arises from the posterior surface of the procerebral lobes (fig. 56, *tri.*) It is indented by a large tracheal tube. From the tritocerebral lobes there arise the roots of two nerves (*r. f. n.*) which pass in front of the œsophagus, join together and form a fine median nerve which runs forwards immediately dorsal to the œsophagus and ends in a small median frontal ganglion, occurring in the plane of the optic lobes (fig. 46, *f. g.*).

Posteriorly the tritocerebral lobes bear a lateral œsophageal ganglion (fig. 46 and 56, *l. œ. g.*), and these two ganglia are connected by a transverse commissure (*tr. c.*) running posterior (ventral) to the œsophagus. At the junction of the tritocerebrum and lateral œsophageal ganglion there is given off on each side a large labral nerve (fig. 56, *la. n.*).

The prothoracic ganglion is separated from the subœsophageal ganglion by only a very short connective, but even this shows division (fig. 46) into right and left.

The nerves for the 1st pair of walking-legs arise latero-ventrally from the prothoracic ganglion. The mesothoracic ganglion is of about the same size as the prothoracic, and the connectives between the two ganglia are nearly double the length of a ganglion and are quite separate from each other.

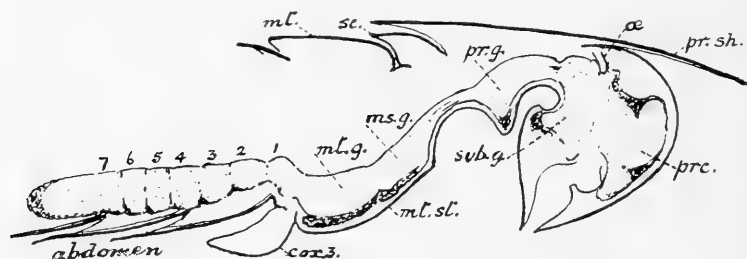
The metathoracic ganglion is somewhat short from back to front, and it is continuous behind with the large elongated abdominal ganglionic mass. The two separate connectives between the meso- and metathoracic ganglia are short, being not more than about half the length of a ganglion. The nerves for the 3rd pair of walking legs arise ventrally from the metathoracic ganglion near its junction with the abdominal mass (Pl. XIX, fig. 46).

The abdominal ganglionic mass lies almost entirely in the thorax and consists of the fusion of a number of abdominal ganglia. From the condition of the supposed larva it is clear that there is a strong tendency for the abdominal chain to shorten and to be drawn forward. In the supposed larva

there are 8 abdominal ganglia, and from the arrangement of the cortex in the fused abdominal mass it would seem that it consists of the remnant of some 7 or 8 ganglia (Pl. XVII, fig. 43). The posterior end of the mass reaches the plane of the middle of the coxa of the last pair of legs, and it tapers only slightly (Pl. XVIII). Laterally the mass gives off a few very fine nerves, but no large nerves, comparable to those supplying the legs, spring from it.

The central nervous system of *Termitomimus* is essentially similar. The procerebral lobes are relatively longer in the antero-posterior axis. The tritocerebrum is not so

TEXT-FIG. 4.



Termitodiscus splendidens Wasm. Longitudinal vertical section showing semi-moniliform condition of abdominal ganglionic mass which extends to the middle of the third abdominal sternite. Lettering as in plates. $\times 140$.

distinctly marked off from the procerebral lobes as in *Paracorotoca*. The prothoracic ganglion is separated from the subesophageal ganglion by a considerable length of double cord. The abdominal ganglionic mass is relatively longer than in *Paracorotoca* (Pl. XVII, cf. figs. 43 and 44).

In *Termitodiscus*, which is a wide, flat form of termitophilous Aleocharine without inversion of abdomen, the central nervous system also shows much modification, but it differs considerably from that of *Termitomimus* and *Paracorotoca*. The prothoracic ganglion is in close contact with the subesophageal (text-fig. 4). There is a moderately long connective between the prothoracic and mesothoracic ganglia.

The meso- and metathoracic ganglia are in close, wide contact with each other. The abdominal ganglionic mass is in direct contact with the metathoracic ganglion. This mass shows much more clearly than in *Paracorotoca* its compound nature, the anterior portion of the mass being almost moniliform. There are 6 obvious ganglia and an end-piece. It is not possible to determine by mere inspection whether the terminal portion consists of one or two ganglia. Judging from the number of ganglia (8) in the supposed larva of *Paracorotoca* this portion is composed of two fused ganglia. The abdominal ganglionic mass is not drawn so far forward as in *Paracorotoca*, since it extends backwards as far as the 3rd or the beginning of the 4th abdominal segment.

Compound Eye.—Externally the eye appears normal in character (Pl. XVI, fig. 7) ; there is considerable development of pigment, and the facettes, which are approximately 120 in number, although large, are less so than in *Termitomimus*. Internally, however, the organ is abnormal, and the ommatidial region is shallow, so that in vertical section the eye is distinctly flat. The flat eye is largely cut off from the inside of the head by a layer of chitin continuous with the general exoskeleton (Pl. XVII, figs. 39 and 40, *i. c.*), and the huge mandibular adductor muscles (*m. m.*) extend slightly on to this chitinous layer. The optic plate (*op. p.*) is degenerate in character, and in the specimen cut into serial sections it had become entirely disconnected from the optic ganglion of the brain (fig. 39, *op. g.*).

The ommatidial elements are remarkably degenerate: there is some remnant of the cone-layer of cells (figs. 41, *d. c. c.*) interspersed with coarse iris pigment-cells (*i. p. c.*), but the layer is almost of the nature of a plasmodium with vacuoles at the periphery. The rhabdome or retinal cells are excessively degenerate (*d. rh. c.*) and are attached to the degenerate optic plate (*d. op. p.*). There is a certain amount of coarse retinal pigment (*r. p. c.*). The general region which should be occupied by the rods is mostly cavity irregularly traversed by protoplasmic strands carrying pigment-cells and also

loose granules of pigment. From the fact that the connection between the optic plate and the optic ganglion of the brain has disappeared it is clear that the insect must be blind; but even if a connective does sometimes persist in certain individuals, yet the condition of the ommatidial elements is such that the eye would be practically useless.

The peculiar condition of some of the cortex cells of the optic ganglion (Pl. XIX, figs. 49, 50, 51, *d. c.*, *d. n. c.*) is very possibly associated with the degeneration of the eye itself.

The compound eye is being gradually cut off from the inside of the head by the ingrowth of the exoskeleton from around the periphery. In fig. 40, *i. cu.*, we see that a portion of the optic plate has been under-cut by this chitin layer secreted by an ingrowth of the general hypodermis (*ec.*). If we imagine this ingrowing of cuticle to continue a little further the eye would be completely cut off from the cavity of the head and would fall away and leave a groove at the side of the head. Such a groove, representing the compound eye, is seen in certain small subterranean beetles, and it is suggested that this eye-less condition has gradually arisen through such a stage as is now present in *Paracorotoca*.

The condition of the eye in *Termitomimus* would seem to be essentially similar. The ommatidial elements, especially the rhabdome cells, are deficient, and the eye is largely cut off from the inside of the head by a remarkably strong chitin layer. The optic plate, however, still retains some connection with the optic ganglion of the brain.

In *Termitodiscus splendidens* we find an analogous condition. The ommatidial elements are densely packed with pigment, and it is necessary to bleach the sections before any cellular structure can be observed. The optic plate (Pl. XVII, fig. 42, *op.*) is very thin and is only connected very inefficiently with the outer edge of the optic ganglion (*op. g.*). The eye is so greatly cut off from the head by ingrowing cuticle (*i. c.*) that there is very little space for an optic plate, and the whole structure appears to have been orientated forwards out of its proper position with reference

to the brain. In bleached sections it is seen that the cellular elements of the ommatidia are quite abnormal (Pl. XIX, fig. 52). There are perhaps remnants of cone-cells (*c. cl.*), but the rhabdome cells bear no distinct rods, and they themselves seem to carry the superabundance of pigment (*p. c.*). Above the optic plate we find large irregular spaces.

The degenerate nature of the eye is perhaps an inherited character which has been gradually evolved either through the direct effect of the darkness of the termite nest on numerous generations, or by the effect of the disuse of the organ. If it were possible to rear an individual in full light the eye might still be degenerate. From the condition of the eye in the imago beetle it may be judged that, just as in the blind fish *Amblyopsis*,¹ the later stages in the differentiation of the retina are cut out of the ontogeny. The final condition of the eye may be regarded as a partial histolysis of a somewhat early developmental stage, and this is accompanied by a tendency to cut off the eye altogether from the body by the development of an ingrowing shelf of chitin.

The loss of eyesight must be to some extent disadvantageous to the insect, especially since for the dispersal of the species wandering from the parent nest must sometimes occur. We cannot, therefore, regard the degeneration as arising through the action of natural selection, but rather as the inherited ill-effect of darkness or disuse. The tendency for the cutting off of the degenerated eye by ingrowing hypodermis secreting cuticle is to be looked upon as a modification of the general tendency of the ectoderm to close up a wound or to pinch off from the body a useless foreign structure.

Olfactory Organs.—Well-developed olfactory pits are present. There is a ring of such round the terminal joint of the antenna, and an especially large oval pit occurs in the end-joint of the palp of maxilla 1. In some sense-organs

¹ Eigenmann, C. H., "The History of the Eye of the Blind Fish *Amblyopsis*," 'Cont. Zoo. Lab. Indiana Univ.,' No. 50, 1903.

(cf. nasal epithelium, lateral line sense-organ) there is a remarkable association of gland-cells and sensory elements; and certain gland-cells mixed with the sensory cells were detected beneath the olfactory pits (Pl. XVII, fig. 23). With the available material and the technique employed it was not possible to determine the exact histological structure of these organs. In the case of the supposed larva, the so-called "olfactory tooth" (which may be really auditory in function) on the antenna showed very clearly the presence of large gland-cells alternating with sensory cells (fig. 23A, *g. c.*).

V. THE SUPPOSED LARVA OF PARACOROTOCOA.

This larva is found in company with the young of the termites. It is probably produced viviparously, since free eggs were never seen, and the smallest larva met with measured about .75 mm. It is presumed that it is born at this size or a little smaller, but doubtless it is not so large immediately on hatching from the egg in the body of the mother. It must be further remarked that in the largest eggs found in the female *Paracorotoca* no definite egg-shell was present, and this fact favours the presumption that eggs are not laid.

The larvæ are much easier to find than the imagos, and they are very certainly much more abundant (Pl. XX, figs. 82, 83).

It is not proposed to describe the various instars; but some account of what appears to be a full-grown larva will be of interest in this place for comparison with the anatomy of the imago of *Paracorotoca*.

1. EXTERNAL MORPHOLOGY.

LENGTH.—Total length of largest larva found about 6 mm.

COLOUR.—Young larvæ milk white, older larvæ pale yellow on those parts where chitinisation becomes fairly dense.

HEAD.—Viewed from in front widely egg-shaped in outline, vertically directed, ventral contour completed by the large, curved pointed mandibles. Labrum, clypeus, frons and genæ

moderately chitinised, occiput covered by two narrow, lateral plates continuous with the genæ. Ocelli very small (*ocl.*), situated laterally behind the antennal pits. Labrum and the general surface of the head, thorax and abdomen bear small, short bristles.

NECK.—Practically absent, the head being in close, wide contact with the prothorax.

THORAX.—Prothorax.—In dorsal or ventral aspect squarish. Two large oval chitinous plates on dorsal surface.

Meso- and metathorax.—Much alike, wider than long, each less than half the length of the prothorax; tergal portion considerably narrower from right to left than sternal and lateral portions, which project on each side and are of about the same width as that of the prothorax. Ventrally a double groove divides the prothorax from the mesothorax; a slightly projecting ridge occurs laterally between the meso- and metathorax (fig. 83).

ABDOMEN.—Widely connected with the thorax. The abdomen is the widest part of the body; when moderately contracted, as in fig. 82, it may be about $1\frac{1}{2}$ times the width of the prothorax. There are 10 abdominal segments; the last three are usually bent ventrally under the front portion of the abdomen (fig. 83). Segments II–VI are provided with conspicuous thin-walled lateral swellings which carry long, thin bristles. Such long bristles also occur on the last three segments of the body.

Antenna.—Of moderate length, it has a singularly large articulating membrane and three joints of very unequal length (fig. 84). The basal joint is somewhat dumb-bell-shaped and bears but few setæ; the 2nd joint is about three times the length of the first, and it is thickest in the middle and carries many setæ; on the inner side terminally it bears a small conical, transparent outgrowth ("olfactory tooth") which is perhaps auditory in function; the apical joint is very small, being about $\frac{1}{4}$ length of the 1st joint, and on the inner side on a step-like notch it carries a long, strong seta. Several other stout setæ are also carried by this joint.

The long seta is undoubtedly an important tactile organ; it is shown in section, together with the "olfactory tooth," in Pl. XVII, fig. 23A.

The antenna of *Corotoca* larva is similar, but the joints are much shorter.

Mandibles.—Pointed, curved, stout, edentulate; closely similar to the mandible of imago; provided with strong muscles (Pl. XX, fig. 86, *md.*).

Maxilla 1.—A large, massive, setose palpiger is fused with the stipes. The palp consists of three rather short, setose joints; the terminal joint is thin and conical and bears a seta in a notch on the outer surface. The stipes also carries a somewhat coarse lacinia bearing a comb of strong setae in an irregular or double row (figs. 85 and 86). This appendage closely resembles that of the larva of *Corotoca* as figured by Schiödt.

Maxilla 2.—Ligula and palpigers form a simple plate carrying a pair of very short, 1-jointed palps on the posterior surface and several setae; mentum bears a number of setae; submentum wide with two setae (fig. 86). In *Corotoca* larva the labial palps are figured as 2-jointed, while in the imago they are 3-jointed; in *Paracorotoca* they are single-jointed in both larva and imago.

Legs.—All three legs are very similar to one another; the 3rd pair are the longest (figs. 87A, B, C). They consist of a short, fairly stout coxa, medium-sized trochanter, and a long femur and tibia. Terminally there is a long, curved claw with a notch on the inner side bearing a bristle. All the joints are setose. In *Corotoca* larva the femur is figured as being relatively very stout, and is only about one-half the length of the tibia, while in *Paracorotoca* larva the femur is only slightly shorter than the tibia.

2. INTERNAL ANATOMY.

Hypodermal Glands.—These are well-developed in the larva. Between abdominal segments III–VIII there are 5 median, dorsal, inter-segmental, deep grooves lined by a tall,

secretory hypodermal epithelium (Pl. XXI, fig. 92). The gland between VI and VII is especially large (*i. g.*) Between segments VIII and IX there is a large dorsal, median hypodermal gland, with a cuticle-lined receptacle opening to the exterior (Pl. XX, fig. 88, and Pl. XXI, *g. r.*); it is of similar structure to that of the pair of glands which occur between abdominal tergites V and VI of the imago (Pl. XVII, fig. 37).

Associated with the hypodermis there are certain huge secretory cells (Pl. XX, fig. 89) which possibly assist ecdysis by pouring a secretion under the cuticle.

Tracheal System.—Not strongly developed. In the thorax there is a fairly large latero-ventrally placed prothoracic spiracle, as in the imago; but no meso- nor meta-thoracic spiracles are present. In the abdomen there are certain minute spiracles which appear to be quite closed by a slightly projecting rod of chitin blocking the end of the tracheal tube (Pl. XX, fig. 89, *sp.*). These spiracles are not lateral, but are placed dorsally, thus foreshadowing their position in the imago. No spiracles could be found on the 1st abdominal segment of the larva, but a pair occurs in each of the segments II–VIII.

The tracheal tubes are embryonic in character and have relatively thick walls composed of peculiarly arranged, flattened cells (Pl. XX, fig. 89, *tr.*, and Pl. XXI, fig. 93, *l. t.*). The lumen, when present at all, may be entirely filled with chitin, but occasionally a little air has been detected in it. The relatively coarse tracheal strands branch but little, and in the abdomen, at least, can have no respiratory function.

Nervous System.—As in the case of the imago, the larval brain was studied by means of a model constructed out of pieces of cardboard cut to shape from serial sections.

The optic ganglion is scarcely distinguishable, but a slight anterior swelling on the outer face of the procerebral lobes doubtless represents it (text-fig. 5, A, *op. g.*).

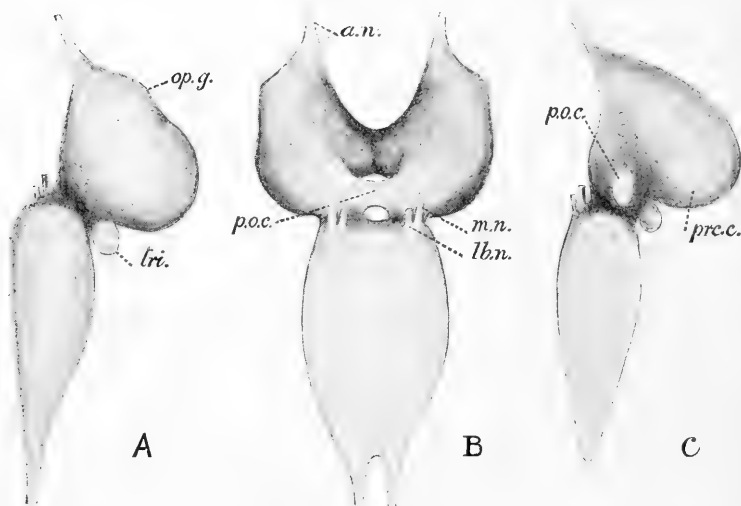
The procerebral lobes bear a marked resemblance in outline to those of the imago; there are the same especially flattened lateral sides and steep posterior rounded surface.

In the mid-dorsal line the transverse commissure between these two lobes is relatively less stout than in the imago (cf. text-fig. 5, c, *prc. c.*, and Pl. XIX, fig. 46).

The antennary lobe and nerve (*a. n.*) are antero-ventral as in imago.

The tritocerebrum (*tri.*) is a small, rounded posterior lobe quite similar in shape and position to that of the imago.

TEXT-FIG. 5.



Larva of *Paracorotoca*. Cephalic nervous system. A. Side view. B. Ventral view. C. Median vertical longitudinal section. *p. o. c.* Postoral commissure. *prc. c.* Procerebral commissure. *m. n.* Maxillary nerve. *lb. n.* Labial nerve. $\times 150$.

The subcesophageal ganglion is of great size as in the imago. There is a postoral commissure (text-fig. 5, B and C, *p. o. c.*) which is doubtless the transverse commissure between the primitive mandibular ganglia. The 1st and 2nd maxillary ganglia are continuous. I am not aware as to whether it has been ascertained that it is usual for full-grown Aleocharine Staphylinid larvæ to retain the primitive condition of possessing a separate mandibular commissure.

The prothoracic ganglion is more widely separated from

the subœsophageal than in the imago. The prothoracic and mesothoracic ganglia are subequal in size, and are joined together by a pair of quite separate, longitudinal connectives. The metathoracic ganglion is smaller than the mesothoracic, and the connectives between them, just as in the imago, are longer than those between the mesothoracic and prothoracic ganglia. The cortex development is weak (Pl. XXI, fig. 92).

There are eight abdominal ganglia, but these are pushed forwards out of their proper segments, and the pairs are placed progressively nearer to each other on passing backwards. Thus the longitudinal connectives are practically absent between the last three pairs of ganglia. The first abdominal ganglia are close to the metathoracic, and the eighth lie between segments V and VI (fig. 92). This forward contraction of the abdominal chain foreshadows the fusion of the abdominal ganglia in the imago.

The Fat-body and Blood-tissue.—The head and thorax of the larva are distinctly broad, while the abdomen is clearly physogastric. None of the internal organs, except perhaps the mesenteron, can be regarded as hypertrophied, but the fat-body is greatly developed in all parts of the body. The fat-cells are mostly arranged in bulky lobules, they are very large and carry numerous fat-globules, while the nucleus is small and often somewhat stellate or polygonal (Pl. XX, fig. 89). In the imago the fat-cells consist of a much denser protoplasm, the nuclei are rounded or oval and larger, and the fat is not carried in the form of discrete, rounded globules (Pl. XIX, fig. 59, *f. b.*). In many parts of the body of the larva there is a distinct tendency for the fat-body to be separated from the hypodermis by a layer of blood containing a few perfectly rounded blood-cells. This character is presented in a marked degree in the exudatory organs or lateral outgrowths from the abdominal segments (Pl. XXI, fig. 93, *ex. o.*). The cuticle of these outgrowths is very thin, and in the distal half there is a considerable blood-space immediately beneath the hypodermis. The Malpighian tubes are surrounded by blood-spaces (fig. 93).

Heart.—A long, dorsal, uniform vessel lying in a special blood-space occurs; it can be traced from the posterior surface of the procerebral lobes to the hinder region of the abdomen; no specially dilated portion appeared to be distinguishable (Pl. XXI, fig. 92).

Alimentary Canal.—Labrum setose, mouth small, pharynx and sucking pharynx essentially similar to those of the imago. The œsophagus is short and narrow throughout, thus differing from that of the imago in not gradually dilating as it passes backwards. There is a small œsophageal valve. The mesenteron commences in the middle of the prothorax (Pl. XXI, fig. 92), while in the imago it begins in the posterior part of the metathorax. The mesenteron of the larva extends through only two abdominal segments, while in the imago it runs through about six.

As in the imago, there are no signs of cæcal glands in the mesenteron.

The ileum in the larva is narrow and relatively long, extending through three segments. At the junction of the ileum with the mesenteron there open dorsally into a little pouch two pairs of Malpighian tubes (Pl. XXI, figs. 92 and 93, *e. ml.*); the width of the tubes at their ends joining the gut is very conspicuously narrower than distally, and such is also the case in the imago. In the imago only two tubes joining the gut could be found. In the case of a male imago *Paracorotoca*, the junctions of the tubes with the gut were so excessively attenuated that there is even reason to speculate whether an appreciable functional aperture was really present. It is just possible that some of the nitrogenous waste is permanently stored in the swollen cells in the distal portions of the Malpighian tubes.

The colon and rectum are relatively short in the larva. In the imago the colon is very large, and replaces the greater part of the ileum of the larva.

In the ventral wall of the rectum near the anus there is a prominent projection covered by an exceptionally high ectodermal epithelium (Pl. XXI, fig. 92, *a.e.o.*). Special

muscles are present, and the structure is doubtless eversible through the anus. The cells appear to be glandular in nature, and the cytoplasm has a very special and characteristic aspect (Pl. XX, figs. 90, 91, *gl. ep.*). Function unknown.

VI. COMPARISON OF LARVA AND PARACOROTOCA IMAGO.

The more important resemblances or differences between this larva and *Paracorotoca* imago may be briefly summarised :

- (1) The larva is an undoubted Staphylinid.
- (2) The larva has 10 abdominal segments, and with Verhoeff's numbering of the abdominal terga in a typical imago beetle we also find 10 segments in *Paracorotoca* imago.
- (3) Exceptional size of palpiger for maxillary palp in both.
- (4) Labial palps 1-jointed in both.
- (5) No salivary glands opening into gut found in either.
- (6) Sucking pharynx in both.
- (7) Oesophagus narrow and short in larva, longer and expanding in the imago.
- (8) Mesenteron of great size in both and carrying no cæcal diverticula in either.
- (9) In larva the ileum is relatively longer and colon shorter than in imago ; 4 Malpighian tubes in larva, only 2 found in imago.
- (10) Fat-tissue of a different type in the larva and in the imago. In the former the fat-tissue is exceedingly abundant, and it occupies the greater part of the space between the gut-wall and the body-wall. The cells are of great size, tend to be arranged in large lobules, and are filled with large globules of fat substance. In the imago the fat-tissue is relatively less abundant ; it occurs in the form of sheets, and the cells are much smaller, stain more readily, and carry the fat-substance in vacuoles of various shapes and sizes.
- (11) In the larva between abdominal segments VIII and IX there is a median dorsal, intersegmental, hypodermal

gland with a receptacle; it is similar in structure to a pair of dorsal hypodermal glands in the imago, which, however, are situated in a different segment of the abdomen.

(12) In the larva the abdominal nerve-chain contains 8 pairs of ganglia, but there is a distinct concentration of the ganglia, and the whole chain is contracted forwards, so that the 8th pair lie in between the 5th and 6th abdominal segments instead of in the 8th segment. In the imago the abdominal nerve-chain is reduced to an elongated mass, consisting of 7 or 8 united ganglia, which has fused on to the metathoracic ganglion.

(13) In the larva there is a postoral commissure immediately behind the œsophagus. This is regarded as the commissure of the mandibular ganglia. In the imago the structure is entirely incorporated in the subœsophageal ganglion.

(14) Abdominal spiracles are dorsally placed in both.

It may be noticed that all the more important differences, such as a more primitive nerve-cord and alimentary canal, are just those which might be expected between a larva and its imago, while the resemblances are very striking. Thus the evidence from the external morphology and internal anatomy is strongly in favour of the assumption, which was so probably on general grounds, that the larva belongs to *Paracorotoca*.

VII. SPECIALISATION ASSOCIATED WITH THE TERMITOPHILOUS HABIT.

The structure of the imago and larva of *Paracorotoca*, as far as it has been ascertained, has now been described, and it is hoped that it will be possible for those who have a wide knowledge of the typical organisation of free-living Staphylinids to form a definite opinion on the nature of the modifications which have resulted from the peculiar environment of a termite nest.

Some of the more obvious peculiarities may be briefly summarised:

(1) The mandibles in both larva and imago are entirely edentulate; they could be used as organs of defence and for piercing prey, but would be quite unsuitable for cutting up prey into small pieces for swallowing.

(2) In both larva and imago the palpiger of maxilla 1 is very large, and its connection with the maxillary palp is so wide that it has the appearance of being the basal joint of the palp itself; the deceptive aspect is further enhanced by a similar distribution of bristles on both palpiger and palp.

In the larva there are 3 joints to the maxillary palp, which is normal, but in the imago there are only 2, although the ordinary number is 4. By comparison with other Staphylinids it would appear that the 1st joint of the palp of the imago *Paracorotoca* has not separated from the palpiger, while the typical 4th joint has disappeared.

The lacinia is typical in the larva. In the imago the lacinia carries a single, horizontally-placed, curved, chitinous spine.

(3) There is great reduction in the 2nd maxilla. Both in the larva and in the imago the palpigers, the ligula and the paraglossæ have fused into a small, median plate which in the imago is slightly bilobed at the apex. The labial palps are reduced to very small 1-jointed structures on the posterior or ventral face. Submentum membranous in the imago.

(4) A sucking pharynx of identical character occurs in both larva and imago. This indicates that in both stages the food is of a fluid nature. A termitophilous habit would appear to render unnecessary the existence of cæcal glands, these being completely absent in the larva and in the imago of *Paracorotoca*; they are also greatly reduced in *Termitomimus*. With the particular kind of fluid food provided a proventriculus is also not required, and it has disappeared completely in both genera. The number of Malpighian tubes has been reduced; for Staphylinids generally, 6 is given for the larva and 4 for the imago, in *Paracorotoca* 4 occur in the larva and apparently only 2 in the imago.

(5) There is an excessive quantity of fat-tissue in the larva

Paracorotoca, a considerable quantity in the imago *Termitomimus* and a moderately large quantity in the imago *Paracorotoca*.

(6) The exudatory structures for producing an agreeable scent or for the passage of fluid licked up by the termites vary in the different forms. In the larva *Paracorotoca* they consist of paired lateral outgrowths of certain abdominal segments. In imago *Paracorotoca* there are (1) a bilobed, median dorsal outgrowth from the front end of prothorax; (2) median swelling of dorsal surface of abdominal segment VIII; (3) paired, backwardly directed swellings from the posterior surface of metathorax. Some similar swellings occur in *Termitomimus*, but (2) is not obviously present and (3) are less strongly developed; Trägårdh believes that fluid also exudes from the ventral, lateral and posterior parts of the rounded, hinder portion of the body.

For the present it cannot be stated whether the inter-segmental glands and eversible anal organ of the larva and the tergal glands of the imago are adaptations to a termitophilous life.

(7) In the female imago *Paracorotoca* there is a long convoluted vagina into which open two thin-walled oviducts bearing a number of ovarian tubes. The ovarian tubes are exceptionally short both in *Paracorotoca* and *Termitomimus*, each tube consisting of about two pairs of elements in the former and usually of only one pair in the latter. The ova grow to a great size and are richly supplied with large yolk-globules. From analogy with *Corotoca*, the absence of any egg-shell and the strong muscular nature of the vagina, it may be concluded that *Paracorotoca* is viviparous. In the male two extremely large follicular testes communicate by means of two short, narrow vasa deferentia with a median, straight, muscular ejaculatory duct; opening into these vasa deferentia are two accessory glands and two large, branched vesiculæ seminales.

Associated with the fact that there is no obvious bursa copulatrix in the female the virgal tube ends in a small,

smooth internal sac, and apparently this cannot be everted very far out of the chitinous penis or middle lobe.

The chitinous penis-tube is very long and can project beyond the head; doubtless copulation takes place in front with the beetles facing each other.

(8) The brain and ventral nerve-cord are very similar in *Paracorotoca* and *Termitomimus*. The cone and rhabdome cells, the optic plate and optic ganglion tend to be defective in both beetles, and this condition is doubtless associated with the absence of an appreciable amount of light in the termite nest.

There is a relative scarcity of cortex in the procerebral lobes, and the mushroom-bodies are poorly developed. It is suggested that the parasitic life has induced a low mental development.

In the full-grown larva *Paracorotoca* there is retained a primitive embryonic condition with reference to the nervous system, in that a mandibular commissure is separate from the suboesophageal ganglion.

In the imago *Paracorotoca* and *Termitomimus* the abdominal nerve-chain is concentrated into a single ganglionic mass which is fused with the metathoracic ganglion.

In the larva *Paracorotoca* there is a more primitive abdominal nerve-chain with separate pairs of ganglia, but they do not lie in their appropriate segments; they are crowded together and are drawn towards the thorax.

(9) Physogastrism is very marked in the imago of both *Paracorotoca* and *Termitomimus*. In the larva *Paracorotoca* it is not so conspicuous, but even here the abdomen is considerably inflated. In the larva the expansion of the body is due to the great development of the fat-tissue and to the large size of the mesenteron. In *Termitomimus* imago it is due to the size of the mesenteron, the amount of fat-tissue and to some extent the hypertrophy of the genital organs. In *Paracorotoca* imago it is due mainly to the hypertrophy of the mesenteron and of the genital organs.

(10) In termitophilous insects there appears to be some

tendency for a reduction in the size of the head; this is seen both in the physogastric and defensive types.

In *Paracorotoca* the head is held downwards at an angle of about 70° – 80° to the horizontal. This feature is less marked in *Termitomimus* and it is not characteristic of Aleocharine Staphylinids.

We now see that *Paracorotoca* exhibits some marked modifications, most of which are shared by other physogastric Staphylinids from Africa, Malay region and South America. These common characteristics do not indicate close genetic affinity, but they are striking examples of the parallelism of structure associated with a similar environment. For example, although *Paracorotoca* in general appearance is extraordinarily like *Corotoca* from South America, yet there are important differences, and in the characters which are commonly used by systematists it appears to be nearer phylogenetically to *Termitoptochus* from the Malay region than to any other described forms, although in general aspect these two beetles are not markedly similar. It is interesting to note that the closer genetic affinity corresponds to a closer geographical connection between the two species.

EXPLANATION OF PLATES XVI—XXI,

Illustrating Dr. E. Warren's paper, "Observations on the Comparative Anatomy of the Termitophilous Aleocharine *Paracorotoca akermani* (Warren)."

EXPLANATORY REFERENCES.

- a.* Aorta. *a. e. o.* Anal eversible organ. *a. g.* Accessory gland. *a. l.* Antennary lobe. *a. m.* Articulating membrane. *a. n.* Antennary nerve. *a. p.* Antennary pit. *ab.* Abdominal nerve mass. *ab. g. m.* Abdominal ganglionic mass. *ab. r.* Abdominal ridge. *ab. s.* Abdominal swelling. *ab. sw.* Abdominal swelling. *al.* Ala. *ao.* Aorta.
- b.* Bridge of procerebral lobes. *b. p.* Basal piece. *bl. t.* Blood tissue.
- c.* Cornea. *c. c.* Procerebral commissure. *c. cl.* Cone-cells. *c. l.* Corpus luteum. *c. p. s.* Reticular cuticle of prothoracic swelling. *ca.*

Cauliculus. *cd*. Cardo. *cg*. Coagulated matter. *cg. m.* Coagulated matter. *ch. p.* Chitinous penis or middle lobe. *cly.* Clypeus. *co*. Cortex. *col*. Colon. *cu*. Cuticle. *cy*. Calyx. *cy. c.* Calyx cells.

d. Discharge pore of mandibular gland. *d. c.* Degenerate cortex. *d. c. c.* Degenerate cone cells. *d. m.* Discharge opening of mandibular gland. *d. ml.* Distal portion of Malpighian tube. *d. n. c.* Degenerate ganglion cells. *d. o.* Developing ovum. *d. op. p.* Degenerate optic plate. *d. rh. c.* Degenerate rhabdome cell.

e. Endoderm. *e. f.* Egg-follicle. *e. ml.* Entrance of Malpighian tube into gut. *e. o.* External opening. *ec*. Ectoderm. *ej.* Ejaculatory duct. *El.* Elytron. *end.* Endostracum. *ep.* Epidermis or hypodermis. *ep. c.* Epithelial cell. *epi.* Epistracum. *ex. o.* Exudatory organ.

f. Food. *f. d.* Female duct. *f. g.* Frontal ganglion. *f. t.* Fat tissue. *f. n.* Frontal nerve. *fr.* Frons.

g. c. Glandular cell. *g. r.* Glandular receptacle. *g. ri.* Gustatory ridge. *gl.* Galea. *gl. c.* Glandular cells. *gl. ep.* Glandular epithelium. *gl. ep. e. o.* Glandular epithelium of eversible organ. *gn.* Gena or cheek.

H. Heart.

i. c. Ingrowing cuticle. *i. g.* Intertergal gland. *i. o.* Internal opening. *i. p. c.* Iris pigment-cell. *i. p.* Iris pigment. *i. s.* Internal sac. *il.* Ileum.

l. l. Labial lobes fused into bilobed plate. *l. l. l.* Left lateral lobe. *l. m.* Longitudinal muscle. *l. m. b.* Locus of mushroom body of brain. *l. n.* Labial nerve. *l. œ. g.* Left œsophageal ganglion. *l. p.* Labial palp. *l. sc.* Layer of digested food being absorbed (?). *l. t.* Larval trachea. *la.* Lacinia. *la. n.* Labral nerve. *lb.* Labrum.

m. Muscle. *m. c.* Muscular coat. *m. d.* Malpighian tube duct. *m. ep.* Mesosternal episternite. *m. g.* Mandibular gland. *m. l.* Muscle layer. *m. m.* Mandibular muscle. *m. n.* Maxillary nerve. *m. s.* Muscular sheath. *m. sh.* Muscular sheath. *md.* Mandible. *md. n.* Mandibular nerve. *me.* Medulla. *mes.* Mesenteron. *mi.* Metasternal epimeron. *ml.* Malpighian tube. *mo.* Mouth. *ms.* Mesonotum. *ms. g.* Mesothoracic ganglion. *ms. s.* Mesosternite. *ms. st.* Mesosternum. *mt.* Mentum. *mt. ep.* Metasternal episternite. *mt. g.* Metathoracic ganglion. *mt. s.* Metasternum. *mt. st.* Metasternum. *mt. sw.* Metathoracic swelling or exudatory organ. *mtn.* Metanotum.

n. Nerve. *n. c.* Nutritive cells. *n. s.* Neck sclerite.

o. Ovum. *o. b.* Olfactory bristle. *o. m.* Ocluser muscle. *o. n. r.* Rudiment of ocellus nerve root. *o. p.* Olfactory pit. *o. t.* "Olfactory tooth." *œ.* Occiput. *ocl.* Ocellus. *œ.* Œsophagus. *œ. ep.* Œsophageal epithelium. *œ. v.* Œsophageal valve. *op.* Optic plate. *op. g.* Optic ganglion. *op. p.* Optic plate. *ov.* Oviduct. *ov. t.* Ovarian tube.

p. Palp. *p. c.* Pigment-cells. *p. ec.* Proctodæal ectoderm. *p. f.* Posterior foramen. *p. fr.* Postfurca. *p. ml.* Proximal portion of Malpighian tube. *p. s. c.* Processes of sensory cells. *p. sp.* Prothoracic spiracle. *p. st.* Prosternal sternella. *pi.* Prosternal epimeron. *plp.* Palpiger. *pr.* Pronotum. *pr. ep.* Prosternal episternite. *pr. epi.* Prosternal epimeron. *pr. g.* Prothoracic ganglion. *pr. p.* Prothoracic dorsal plate. *pr. sh.* Prothoracic shield. *pr. sw.* Prothoracic swelling or exuding organ. *pre.* Procerebral lobe. *prst.* Prosternum. *pst.* Acro- and prosternite.

r. Rectum. *r. f. n.* Root of frontal nerve. *r. l. l.* Right lateral lobe. *r. œ. g.* Right œsophageal ganglion. *r. p.* Retinal pigment. *r. p. c.* Retinal pigment cell. *ret. t.* Reticular tissue. *rp.* Receptacle.

S. Sternite. *s.* Sensory cell. *s. c.* Seminal chamber. *s. ch.* Seminal chamber. *s. d.* Seminal duct. *s. d. f.* Semi-digested food. *s. ep.* Secretory epithelium. *s. mt.* Submentum. *s. ph.* Suctorial pharynx. *s. w.* Striated wall of spermatheca. *sc.* Scutellum. *se.* Semen in spermatheca. *sec.* Secretion. *sh.* Sheath cavity of male sexual apparatus. *sp.* Spiracle. *spi.* Spine. *spt.* Spermatheca. *spz.* Spermatozoon. *stp.* Stipes. *sub. g.* Subœsophageal ganglion.

T. Tergite. *t.* Testis follicle. *t. b.* Tactile bristle. *t. m.* Transverse muscle. *tr.* Trachea. *tr. c.* Transverse commissure between œsophageal ganglia. *trb.* Trabecula. *tri.* Tritocerebrum. *tri. c.* Trichogenic cell. *tric.* Trichome.

V. Vertex. *v. c.* Vacuolated cell. *v. s.* Vesicula seminalis. *va.* Vagina. *vac.* Vacuole.

y. f. Young follicle. *y. p.* Yellow spot on abdomen.

PLATE XVI.

FIG. 1.—× 35. Side view of the beetle *Paracorotoca akermani* (Warren), with the right side of the inverted abdomen slightly raised to show the tergites between the longitudinal ridges. Note the exudatory structures, *pr. sw.*, *mt. sw.* and *ab. sw.*, the supposed sexual recognition-gland underneath sternite IX, and the spermatheca lying beneath the cuticle in segment VIII.

FIG. 2.—× 35. Ventral view of the male beetle. The sexual apparatus is everted with the chitinous penis or middle lobe in the mid-line, while the paramera or lateral lobes are obliquely dorso-ventral in position. The ventral thoracic sclerites, the articulations of the walking legs and the "abdominal stalk" are visible.

FIG. 3.—× 35. Dorsal view of a female beetle, with the abdomen stretched backwards in line with the thorax. Note the two longitudinal,

abdominal ridges, the peculiar abdominal tergites of different shapes, and the dorsal position of the spiracles. The numbering of the segments follows the scheme given by Berlese.¹ The bilobed nature of the prothoracic swelling (*pr. sw.*) is shown.

FIG. 4.— $\times 75$. Front view of head, showing setose labrum, ventral, membranous portion of clypeus (*cly.*), discharge pore (*d.*) of mandibular gland, antennal pits, and the two concavities of occiput (*oc.*) in which the bilobed prothoracic swelling is lodged.

FIG. 5.— $\times 75$. Side view of head, showing huge palpiger (*plp.*) and 2-jointed maxillary palp (*p.*).

FIG. 6.— $\times 75$. End-on view of head, showing cheeks (*gn.*) and mouth-parts.

FIG. 7.— $\times 75$. Back (ventral) view of head, showing mouth-parts in situ. Labial palp (*l. p.*) is one-jointed.

FIG. 8.— $\times 75$. Isolated tergite of 2nd abdominal segment. X-shaped sclerite with the two limbs on each side connected by a curved plate of chitin; one pair of limbs clasps the abdominal stalk and the other supports the angle of the upturned portion of the abdomen. The latter are perforated by the 2nd pair of abdominal spiracles.

FIG. 9.— $\times 375$. Longitudinal vertical section of body through one of the typical abdominal sternites, showing its subdivisions (*pst. ms. s.* and *mt. s.*) and relationship to the general cuticle (*cu.*) of the body. It is clear that the sclerites are to be regarded merely as areas of concentrated chitin within the general cuticle.

FIG. 10.— $\times 90$. Left view of partially extruded sexual apparatus of the male. The internal sac (*i. s.*) issuing from the chitinous penis (*ch. p.*) or middle lobe is the distal end of the ejaculatory duct. Lateral lobes are obliquely placed, the right one (*r. l. l.*) being ventral and the left (*l. l. l.*) dorsal. Two horseshoe-shaped chitinous pieces at the base of the lobes may be perhaps regarded as representing tergite X.

FIG. 11.— $\times 70$. Right view of extended male apparatus. Segment X bears two lateral setose plates apparently representing the 10th sternite.

FIG. 12.— $\times 70$. Left view of extended male apparatus, showing the so-called "basal piece" (*b. p.*) of Sharp and Muir.

FIG. 13.— $\times 70$. Dorsal view of extended male apparatus.

FIG. 14.— $\times 70$. End-on view of extremity of female abdomen, showing the divided 10th sternite above and the median 10th tergite below.

FIG. 15.— $\times 90$. End-on view of extremity of female abdomen.

¹ Berlese, Antonio, 'Gli Insetti,' p. 266. Milan, 1909.

showing extruded vagina and two small, obliquely-placed processes, probably to be regarded as homologues of the lateral lobes of the male.

FIG. 16.— $\times 70$. Left view of extremity of female abdomen, showing position of supposed recognition-glands (*r. g.*).

FIG. 17.— $\times 70$. Left view of extremity of the abdomen of female, with extruded vagina and lateral lobes.

FIG. 18.— $\times 70$. Right view of the same.

FIG. 19.— $\times 100$. Transverse section through male beetle in the plane of the metathorax and the sixth abdominal spiracle. Abdomen largely filled by the hypertrophy of the testes (*t. f.*) and of the colon (*col.*). Posterior narrow end of mesenteron pushed dorsal to (below) colon, while in two females examined it remained entirely ventral (above). Note the longitudinal abdominal ridges which rest on the elytra of the thorax.

PLATE XVII.

FIG. 20.— $\times 60$. Antenna of beetle with large, proximal, articulating membrane and 11 joints. The terminal joint is provided with a median ring of olfactory pits.

FIG. 21.— $\times 140$. Side view of mandible.

FIG. 22.— $\times 140$. Frontal view of maxilla 1. Note large palpiger and the 2-jointed palp. On the second joint occurs a well-developed large sense-pit, containing olfactory bristles.

FIG. 23.— $\times 950$. Vertical longitudinal section of olfactory pit of maxillary palp. Note olfactory bristles (*ob.*), sensory and nerve-cells, and certain vaguely-defined secretory cells.

FIG. 23A.— $\times 350$. Terminal portion of antenna of supposed *Paracrotoca* larva, showing a well-developed tactile bristle and on one side a conical "olfactory tooth." Note gland-cells (*g. c.*) mixed with sensory cells (*s.*).

FIG. 24.— $\times 140$. Back (ventral) view of maxilla 2. The lateral lobes have fused into a slightly bilobed plate bearing small 1-jointed palps; a well-defined mentum below.

FIG. 24A.— $\times 175$. Mouth and portion of labrum in vertical longitudinal section. Note labial nerve (*l. n.*), setose condition of inner surface of bilobed plate, and a lateral setose ridge (*g. r.*) which is possibly gustatory. The two lateral ridges perhaps represent portions of a median epipharynx.

FIG. 25.— $\times 45$. Ventral view of prothoracic leg, showing articulation and surrounding prothoracic sclerites.

FIG. 26.— $\times 350$. Side view of claws of prothoracic limb.

FIG. 27.— $\times 45$. Side view of mesothoracic leg, showing articulation and surrounding sclerites.

FIG. 28.— $\times 45$. Ventral view of metathoracic leg, showing articulation and sclerites.

FIG. 29.— $\times 60$. Ventral view of left elytron.

FIG. 30.— $\times 250$. Vertical longitudinal section of prothoracic exudatory organ, showing thick, soft, permeable cuticle.

FIG. 31.— $\times 120$. Vertical transverse section of prothoracic exudatory organ resting on occipital region of head.

FIG. 32.— $\times 180$. Vertical longitudinal section of metathoracic exudatory organ, showing on one side much coagulated matter (*cg. m.*) between the cuticle and the epidermis.

FIG. 33.— $\times 180$. Vertical longitudinal section through the median abdominal exudatory organ.

FIG. 34.— $\times 250$. Vertical longitudinal section through the ventral body-wall of the prothorax, showing the curious crumpling.

FIG. 35.— $\times 500$. Vertical section through the lateral body-wall of metathoracic region, showing the peculiarly porous nature of the endostracum, and a considerable amount of coagulated matter between cuticle and hypodermis.

FIG. 36.— $\times 400$. Transverse section through cephalic glandular epithelium (*gl. ep.*), showing a bilobed condition.

FIG. 37.— $\times 500$. Vertical longitudinal section through lateral tergal gland, showing mass of secretion (*se.*) in the receptacle (*R.*).

FIG. 38.— $\times 500$. Vertical longitudinal section through trichome and body-wall, showing trichogenic cell (*tri. c.*) and the communication with the exterior, around the base of bristle, of the space between the cuticle and the epidermis.

FIG. 38A.— $\times 250$. Spiracle opening on tergum IX, seen from the outside.

FIG. 39.— $\times 325$. Vertical cross-section of head, showing the disconnection of the optic (*op. g.*) ganglion of the brain and the optic plate (*op. p.*) of the compound eye. Note the degenerate character of the ommatidia and the ingrowing cuticle (*i. c.*) tending to cut off the eye from the inside of the head.

FIG. 40.— $\times 325$. Section through the eye, less central than that of fig. 39; here the ingrowing cuticle (*i. cu.*) forms a continuous partition.

FIG. 41.— $\times 800$. Vertical section of portion of degenerate compound eye showing abundance of pigment, but cone-cells, and especially the rhabdome cells, are very degenerate.

FIG. 42.— $\times 225$. Vertical section of portion of head and prothoracic shield of *Termitodiscus splendidus* Wasm. Given for comparing the structure of the eye. Note abundance of pigment, degenerate optic plate almost separated from optic ganglion, and the encroaching cuticle tending to cut off the eye.

FIG. 43.— $\times 55$. Side view of central nervous system of *Paracorotoca akermani*. Note tritocerebrum with large tracheal tube.

FIG. 44.— $\times 85$. Side view of central nervous system of *Termitomimus entendveniensis* Träg. Given for comparison.

PLATE XVIII.

FIG. 45.— $\times 65$. Semi-diagrammatic vertical longitudinal section of female *Paracorotoca* beetle. The numbering of the segments is based on the supposition of ten abdominal segments.

PLATE XIX.

FIG. 46.— $\times 100$. Dorsal view of central nervous system of *Paracorotoca*. Note tritocerebrum (*tri.*), large tracheal tube, œsophageal ganglion (*r. œ. g.*), frontal ganglion (*f. g.*).

FIG. 47.— $\times 100$. Side view of brain and subœsophageal ganglion.

FIG. 48.— $\times 100$. Ventral view of brain and subœsophageal ganglion.

FIG. 49.— $\times 170$. Vertical cross-section of front portion of optic ganglion, showing peculiar small, solid nuclei (*d. c.*) without cell outlines, possibly indicating degeneration associated with the abortion of the eye.

FIG. 50.— $\times 170$. Vertical section a little behind that of fig. 49, showing the beginning of the antennary lobe (*a. l.*).

FIG. 51.— $\times 170$. Vertical section through the procerebral lobes and front portion of subœsophageal ganglion, showing origin of mandibular nerve.

FIG. 52.— $\times 250$. Vertical section through brain and compound eye of *Termitodiscus splendidus* Wasm. Bleached with chlorine.

FIG. 53.— $\times 170$. Vertical cross-section through the middle of the procerebral lobes. Note the scarcity of nerve-cells or cortex, the medulla (*me.*) forming the bulk of the structure. The origin of nerve to maxilla 1 is seen.

FIG. 54.— $\times 170$. Vertical cross-section near the posterior vertical face of procerebral lobes. Note the trabecula (*tr. b.*), calyx (*cy.*), cauliculus (*ca.*), and bridge (*b.*) of procerebral lobes. The origin of labial nerve (*l. n.*) is seen.

FIG. 55.— $\times 170$. Cross-section immediately behind that of fig. 54,

still showing calyx (*cy.*) in the cortex. Note frontal nerve (*f.n.*) immediately dorsal to œsophagus.

FIG. 56.— $\times 170$. Vertical cross-section a little posterior to that of fig. 55. Only the cortex of the posterior periphery of the procerebral lobes is seen. The origin of the tritocerebrum and lateral œsophageal ganglia is shown. A transverse commissure (*tr. c.*) running ventral to the œsophagus connects the œsophageal ganglia of the two sides. The roots of the frontal nerve are seen dorsal to the gut, and the labral nerve (*la. n.*) is also seen.

FIG. 57.— $\times 700$. Mandibular gland in section, consisting of large glandular cells, with exceptionally large nuclei and no obvious cell outlines. The secretion apparently exudes at a spot (*d. m.*) situated between the mandible and maxilla 1.

FIG. 58.— $\times 500$. Cross-section of œsophagus in hinder region. Some of the ectodermal epithelial cells (*œ. ep.*) are provided with long spines (*spi.*) radiating to the centre and forming an efficient strainer, through which passes the coarsely granular food (*f.*).

FIG. 59.— $\times 500$. Vertical longitudinal section through the body-wall and middle portion of mesenteron in a female. The cells of the endoderm (*e.*) are of very unequal height and there are large vacuolated cells. The food has become somewhat less stainable and is less coarsely granular than that in the œsophagus.

FIG. 60.— $\times 240$. Cross-section of middle region of mesenteron of a male, showing crumpled wall, vacuolated cells discharged bodily into the semi-digested food, a continuous layer of substance (*l. c.*) (digested food being absorbed?) on the inner surface of the epithelium, and a number of deeply staining gland-cells wedged at the base of the epithelium. The food in the lumen has become highly vacuolated, very finely granular, and stains but little.

FIG. 61.— $\times 500$. Cross-section of anterior narrow portion of colon, with large irregularly shaped ectoderm cells and no obvious cuticle.

FIG. 62.— $\times 500$. Longitudinal section of posterior portion of colon, with small irregularly shaped cells, which may exhibit considerable chitinisation.

FIG. 63.— $\times 37$. Male genital organs. The illustration was prepared from a series of sketches made from a good set of serial sections. The seminal ducts and ducts of the branched vesiculæ seminales and of the unbranched accessory glands open close together at the anterior end of the ejaculatory tube.

FIG. 64.— $\times 650$. Cross-section of a portion of the accessory gland, showing an epithelium of peculiarly slender, tall cells. The thick

secretion (*sec.*) would appear to arise as an actual transformation of the protoplasm of the whole of the inner portion of the epithelium.

FIG. 65.— $\times 500$. Section of portion of the vesicula seminalis. Epithelium is very thin, nuclei very indistinct, and the cells appear to be almost chitinised in nature.

FIG. 66.— $\times 80$. Cross-section of posterior extremity of abdomen of male, showing structures in genital vestibule.

FIG. 67.— $\times 80$. Cross-section a little anterior to that of fig. 66, showing the dorsal and ventral position of the "lateral lobes" (Sharp & Muir) (*l.l.l.* and *r.l.l.*) within the sheath (*sh.*) of the external genital apparatus.

FIG. 68.— $\times 90$. Semi-diagrammatic side view of the partially extruded external genital apparatus of the male.

FIG. 69.— $\times 200$. Cross-section of male genital apparatus, showing the origin of the lateral lobes from the wall of the sheath.

FIG. 70.— $\times 200$. Cross-section of apparatus through the middle of the swollen portion of the chitinous penis ("middle lobe" of Sharp and Muir). The sheath is provided with powerful longitudinal and oblique muscles. The chitinous penis is lined internally by hypodermis, while remains of hypodermis may also be found on the inner surface of the cuticle lining the sheath.

FIG. 71.— $\times 200$. Cross-section of apparatus, showing the entrance of the ejaculatory duct (*ej.*) into the chitinous penis.

FIG. 72.— $\times 200$. Cross-section through chitinous penis in front of the pore of entrance of the ejaculatory duct.

PLATE XX.

FIG. 73.— $\times 450$. Section through two follicles of testis, that on the left being a young follicle (*y.f.*), showing the formation of the spermatocytes. The epithelium of the internal sperm-chamber (*s.ch.*) of the testis is modified into a curious channelled or reticular tissue (*ret.t.*) opposite each follicle. The ripe spermatozoa (*sp.*) penetrate through the tissue.

FIG. 74.— $\times 600$. Piece of typical fat tissue from the thorax of the beetle.

FIG. 75.— $\times 35$. General dorsal view of the female genital apparatus. The drawing is constructed from a set of serial sections. Note the two irregular thin-walled oviducts joining a median thick-walled vagina, provided with accessory glands (*gl.c.*) near the external aperture. In all the individuals sectioned the duct connecting the spermatheca with the vagina could not be found. It is surmised that this duct may atrophy after copulation has occurred.

FIG. 76.— $\times 200$. An ovarian tube, showing a corpus luteum (*c. l.*) where an egg has matured. A mass of nutritive cells surmounts each ovum. An ovum beginning to be differentiated is seen at *d. o.*

FIG. 77.— $\times 200$. Another ovarian tube with a large ovum surrounded by its follicle.

FIG. 78.— $\times 400$. Cross-section of vagina near the external opening.

FIG. 79.— $\times 150$. Vertical longitudinal section of the ventral portion of the posterior extremity of the female abdomen. Note the mass of gland-cells pouring a secretion into the recess lying above sternum X. The gland and recess are lateral and paired. Possibly the gland secretes a fluid for sexual recognition.

FIG. 80.— $\times 150$. Cross-section through the front portion of segment X, showing accessory gland (*gl. c.*), practically continuous with recognition-gland (*gl. r.*). The secretion (*sec.*) of the accessory gland is shown.

FIG. 81.— $\times 550$. Section through spermatheca as it is issuing from the spermathecal gland. Semen from copulation is seen in the spermatheca, which is internally ridged like a trachea. It is presumed that the spermathecal gland pours a secretion into the spermatheca for maintaining the spermatozoa in an efficient condition.

FIG. 82.— $\times 20$. Dorsal view of the presumed full-grown larva of *Paracorotoca*. Note the paired abdominal lateral exudatory organs, the minute ocellus and the "olfactory tooth" at the distal end of the 2nd joint of the antenna. The articulating membrane (*a. m.*) of the antenna with the head is so wide as to mimic an additional joint.

FIG. 83.— $\times 20$. Ventral view of the larva. Note supra-anal plate on segment X surrounded by a ring of setæ.

FIG. 84.— $\times 50$. A right antenna. The terminal bristle of the 3rd joint would appear to be an especially delicate tactile organ.

FIG. 85.— $\times 85$. Inner view of maxilla 1, showing lacinia (*la.*), a huge palpiger (*pl.*) fused with the stipes, and a 3-jointed palp.

FIG. 86.— $\times 85$. Posterior view of the mouth-parts of the larva in situ. Note maxilla 1 with ligula, palpigers and labial lobes fused into a median plate bearing a 1-jointed palp (*p.*).

FIG. 87A.— $\times 30$ and 150. Prothoracic leg of larva, with an enlarged view of terminal claw.

FIG. 87B.— $\times 30$ and 150. Mesothoracic leg and claw.

FIG. 87C.— $\times 30$ and 150. Metathoracic leg and claw.

FIG. 88.— $\times 600$. Median vertical section through the median tergal gland and its receptacle of the larva, situated between segments VIII and IX. Note that the fat tissue has stellate small nuclei and large globules of fat; compare with fig. 74.

FIG. 89.— $\times 600$. Vertical section through an abdominal spiracle and tracheal tube of the larva. An actual perforation was not demonstrated. Note the peculiar large cells forming the wall of the trachea and the huge secretory cells in contact with the hypodermis.

FIG. 90.— $\times 600$. Median vertical longitudinal section of the larva through the anus and a peculiar eversible organ with tall glandular cells (*gl. ep. e. o.*). Compare anal eversible organ (*a. e. o.*) in fig. 92.

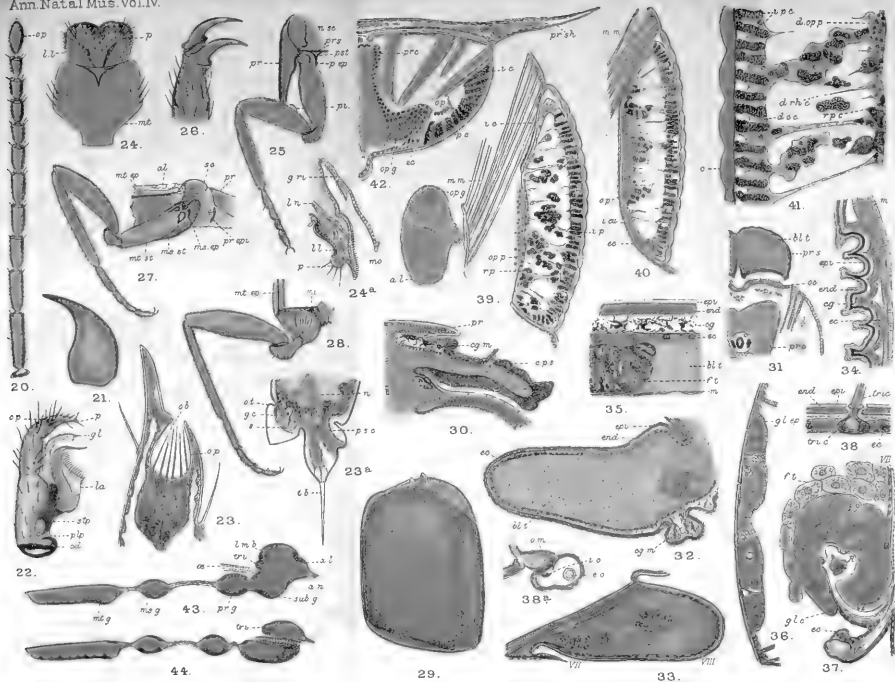
FIG. 91.— $\times 450$. Transverse section through larva in the plane of the eversible organ.

PLATE XXI.

FIG. 92.— $\times 70$. Semi-diagrammatic view of a median vertical longitudinal section of the larva. Note that the abdominal ganglia are drawn forward and do not lie in their appropriate segments; e.g. the eighth ganglion (*g. 8*) lies in abdominal segment VI. The mandibular commissure (*m. c.*) is seen. The condition of the imago is foreshadowed in the larva by the character of the alimentary and nervous systems, which are, however, less specialised.

FIG. 93.— $\times 85$. Transverse section through the abdominal region of the larva. Note the entrance of a Malpighian (*e. ml.*) tube into the gut, and the exudatory organs (*ex. o.*). Tracheal tubes (*l. t.*) are apparently in the course of formation.



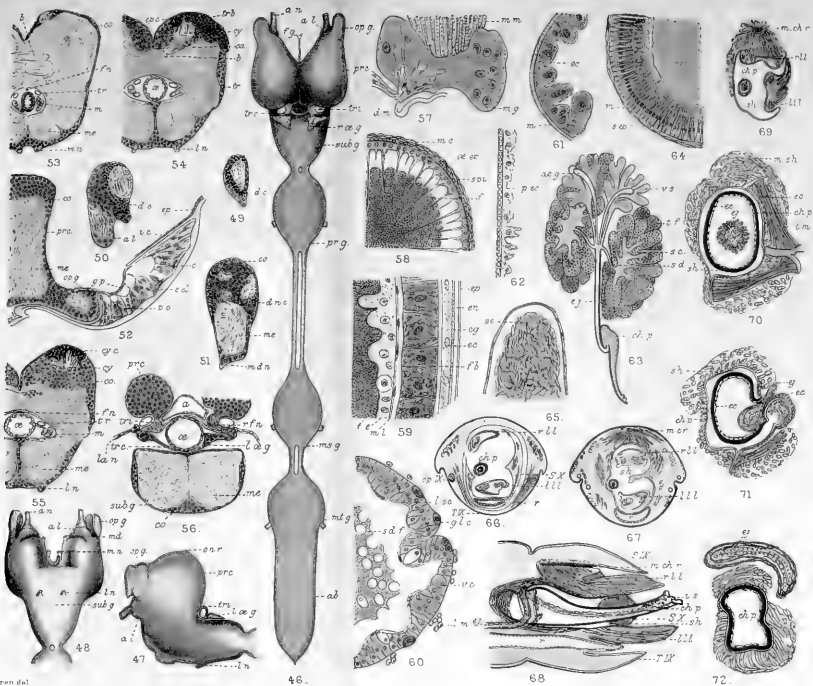


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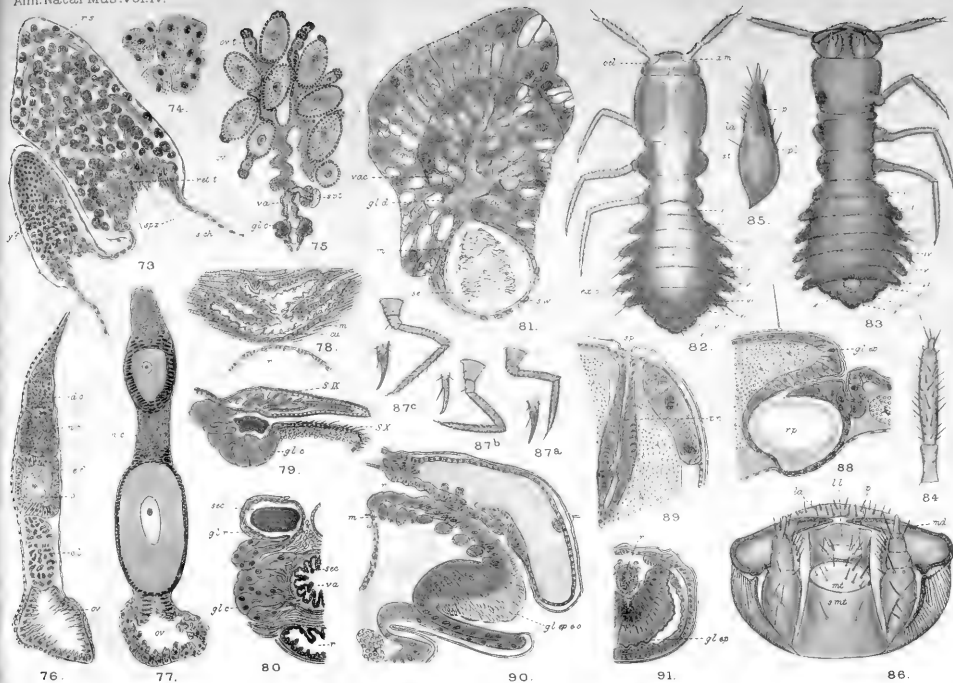






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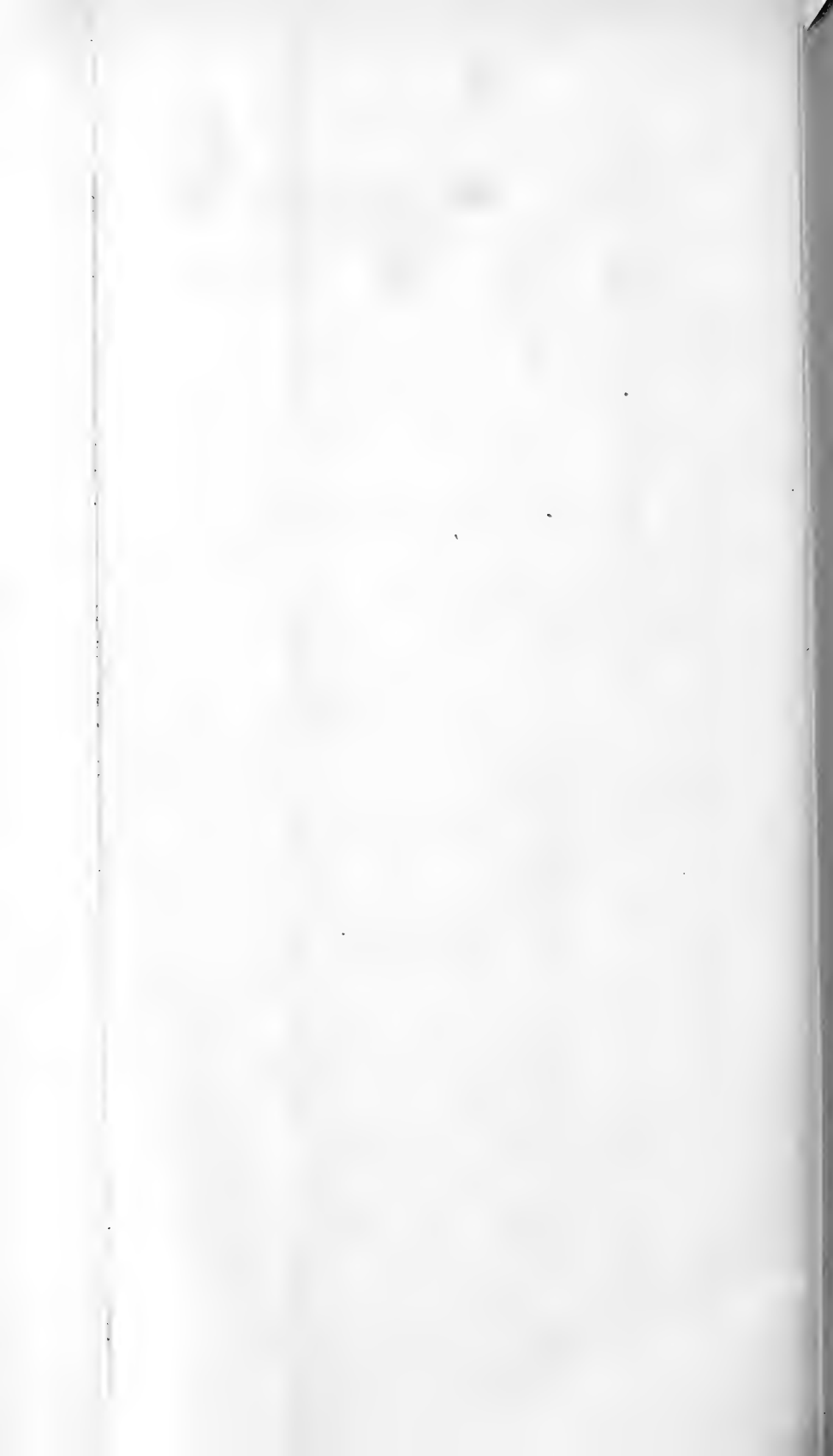


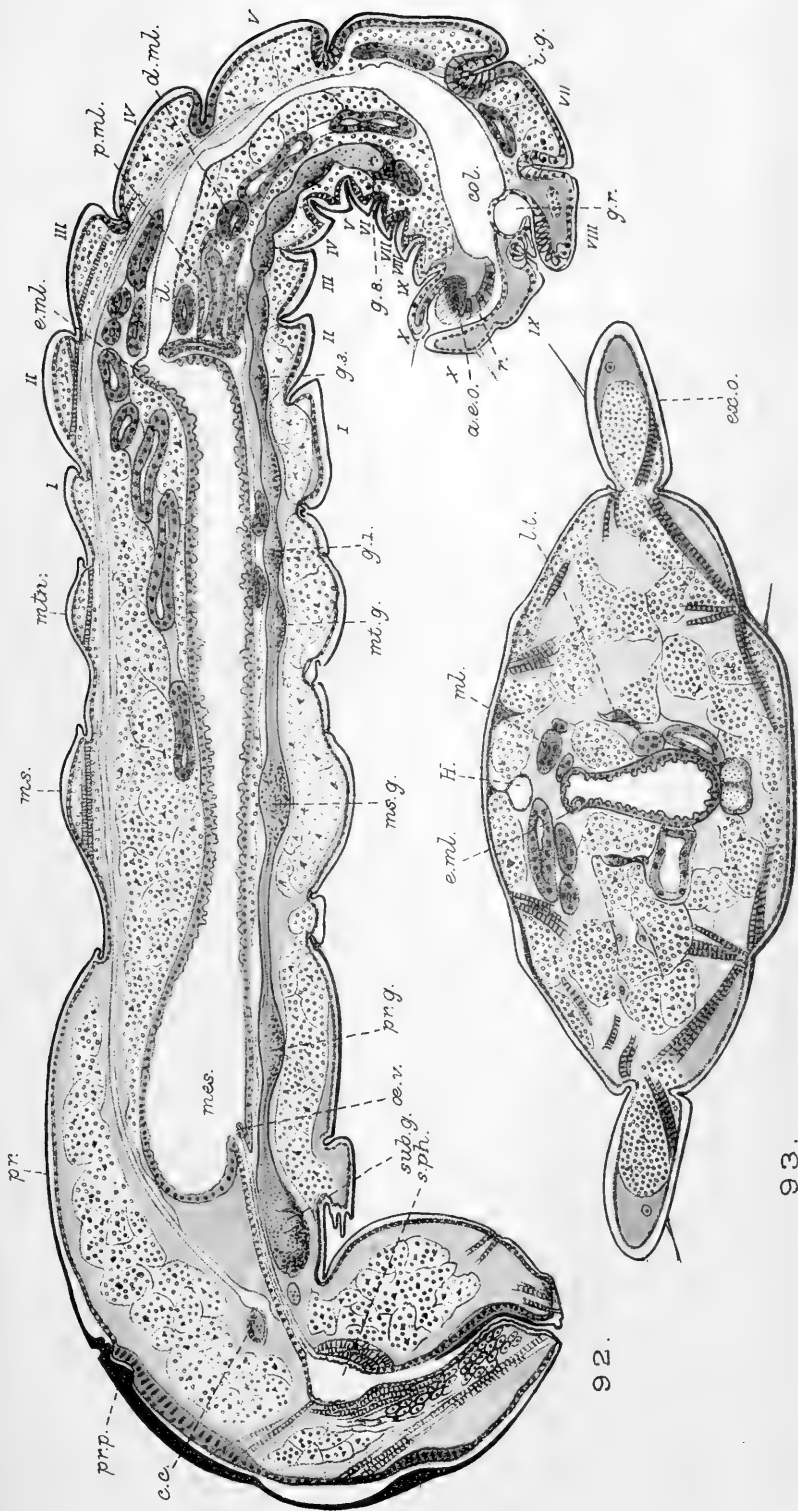


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The Plant Ecology of the Coast Belt of Natal.

By

J. W. Bews, M.A., D.Sc.,

Professor of Botany, Natal University College.

With Plates XXII-XXVI, and 4 Text-figures.

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INTRODUCTION.

THE following paper is the fourth of a series published in this Journal on the plant ecology of Natal. The first¹ was a general account of the vegetation of Natal as a whole, the second² gave a detailed survey of a portion of the Midlands, the third³ dealt with the Drakensberg range. The general topographical map published in the first paper of the series will be found useful for reference, since the extent of the coast-belt area is shown on it. As the study of the vegetation of Natal and other parts of South Africa has progressed I have been able to give more attention to the analysis of the plant succession, and the present paper is arranged in such a way as to make this as clear as possible. In a recently published work⁴ I adopted the system of nomenclature of Clements in his book on "Plant Succession." I have found that it can be applied equally successfully to a subtropical area such as the Natal Coast belt, and I have therefore continued to use it.

I have to acknowledge generous assistance from Mr. J. S. Henkel, who supplied me with a list of trees and shrubs occurring at Umgababa, as well as a list of Zulu plant names, and who has also brought to my notice many interesting points; and from Dr. T. R. Sim, who assisted in many difficult decisions regarding the relative frequency of various species. I am indebted to Miss K. Martindale for drawing text-fig. 1 and to Mr. R. Walker for re-drawing fig. 3.

While the ecological study of the coast-belt has been continued at intervals since 1910, during this year (1919) it has

¹ Bews, J. W., "The Vegetation of Natal," 'Annals of the Natal Museum,' vol. ii, p. 253, 1912.

² Bews, J. W., "An Œcological Survey of the Midlands of Natal," *ibid.*, vol. ii, p. 485, 1913.

³ Bews, J. W., "The Plant Ecology of the Drakensberg Range," *ibid.*, vol. iii, p. 511, 1917.

⁴ Bews, J. W., 'The Grasses and Grasslands of South Africa,' Pietermaritzburg, 1918.

formed part of the work done for the Botanical Survey of the Union, recently instituted under the directorship of Dr. I. B. Pole-Evans.

The following section on the geology, topography, and soil-conditions has been very kindly supplied by Dr. A. L. du Toit, who has carried out the recent detailed geological survey of most of the coast belt.

I. GEOLOGY, TOPOGRAPHY, AND SOIL-CONDITIONS.

The hundred and fifty miles of low-lying coastal belt in Natal possess a wonderful uniformity, which can in part be accounted for by the fact that climatically there is little variation from south to north within this stretch of country. The straight north-easterly trending coast-line, broken only by Port Natal, has been determined mainly by down-warpage of the seaward side of Natal in Cretaceous times along a nearly parallel hinge-line, situated some distance inland, such having been accompanied by minor folding and by considerable faulting in the coastal portion. The sculpturing of the surface is of the same pattern throughout, and the general slope for a short distance back has a value of between $1\frac{1}{2}$ and 3 degrees, so that the thousand-foot contour is attained within from 5 to 10 miles usually, though the gradient over the next thousand feet is less. The rivers are arranged at right angles to the coast-line, and taken in order from south to north consist of the Umtamvuna, Umzinkulu, Umzumbi, Umtwalumi, Umzinto, Unkomaas, Illovo, Umlazi, Umgeni, Umhloti, Tongaat, Umvoti and Tugela. They have cut deeply into the general surface and flow in picturesque gorges, between each pair of which the ground generally rises rather regularly inland, advantage having been taken of this fact in the construction of roads and railways. Occasionally ground belonging to the coastal belt and well below the thousand-foot contour is partially or wholly severed from the dissected plateau inland, as, for example, within the Umtwalumi valley.

With the marked exception of the Table Mountain Sandstone the topographical pattern is practically independent of the geological formation, such being due in great degree to the high rainfall, coupled with the ubiquitous growth of vegetation; rarely, indeed, are bare surfaces of rock exposed on hillsides upon a large scale. The topography is of the youthful type, the valleys tributary to those of the main rivers being steeply graded, crooked and steep-sided with V-shaped cross-sections, while the watersheds are narrow, sinuous and hummocky, often to an extraordinary degree; as a rule the pattern is more elaborated, but on a smaller scale, the nearer the shore. The actual heads of many of the smaller streams are phenomenally steep-sided, the hollows being lined with bush; the sapping effect of the percolation has obviously been responsible for the development of the hollow, and the vegetation brought about thereby for its maintenance.

The Table Mountain Sandstone (Devonian) is the most distinctive formation in Natal. Owing to its hardness and horizontal or gentle seaward dip it has produced scarped plateaux, or else terraced surfaces that slope seawards, and are rather scantily forested as a rule. Outlying masses, unconformable upon a granite base, are conspicuous in the area extending between the coastal patches of this formation and the more continuous capping of the 2,000–2,500 foot plateau, for example, in the neighbourhood of Umzinto. In this latter region, however, flat-topped ridges are also found, composed, not of sandstone, but of a pale granite. Under weathering each formation furnishes a more or less distinctive type of soil.

The granites yield good soils of generally coarse character containing fragments of more or less kaolinised felspar, the latter tending to supply a clayey base. The more gneissose hornblendic varieties give deep red soils of finer texture, for instance, on the south side of the Umzumbi and in the middle reaches of the Umpambinyoni River. On steep slopes bare surfaces of granite frequently project through the scrub, e.g.

in the Umzinkulu, Umzinto and Illovo valleys, while now and then domes of solid rock are seen rising out of relatively even country.

The Table Mountain Sandstone yields a rather pale grey or pinkish open sandy soil with small white quartz pebbles; this is distinctly poor and sour—a defect intensified by the occasional development of a layer of hard lateritic ironstone just beneath the surface. When the formation constitutes a plateau, the smaller streams arising thereon generally flow in shallow channels along which there are lengths characterised by rocky bars alternating with sections possessing a black, sandy and often boggy soil.

The succeeding Dwyka Conglomerate varies greatly in its surface habit. In its usual decomposed state it gives a pale sandy to clayey soil with scattered boulders, and the spheroidally weathering and buff-coloured crumbly rock beneath is easily penetrated by the roots of trees, but on ridges and steep slopes the conglomerate may crop out in bare, grey slabby or hummocky surfaces, rough by reason of the projecting inclusions, the rock being intensely hard and dark blue in colour. In such situations the ground tends to be treeless as on the 800–1000-foot plateau between the Umkomaas and the Umpambinyoni rivers.

The still younger blue (Lower) Ecca Shales, pierced by dolerite sheets roughly following the bedding planes, crumble away on the other hand to drab chocolate or red clayey soils, while the succeeding (Middle) Ecca “Coal Measures” give paler, more open-textured and sandy varieties. The dolerite sheets penetrating these two groups have a very marked influence, firstly, in producing a more fertile soil, either deep red in colour or blackish, powdering when dry, but tenacious when wet, and secondly, by reason of its water-storing qualities in keeping the soil moist, the soakage from the rainfall making its way along the contact of the decomposed and jointed igneous rock with the underlying indurated shales. This is so frequently the case that the course of such a sheet on a hilly and overgrown area can, not uncommonly,

be at once determined by the presence of certain scrub-filled hollows on the flanks of the ridges in contrast to the barer and smoother slopes of shales above and below.

The most important feature, however, of the coastal belt is the mantle of blown sand that almost invariably conceals the geological structure over a tract extending inland a distance of from half a mile up to two or even three miles from the shore. Inland this covering is scanty and confined to the ridges, but upon approaching the shore the mantle becomes thicker and more continuous, so that the nature of the underlying strata can only be gathered from scanty exposures along the stream courses, though sometimes for intervals of over a mile there may be no outcrops.

Along the beach and occasionally bordering the lagoons there are practically continuous surfaces of rock to just above high-water mark, behind which the sand builds up one or more tiers of scrub-covered dunes. These are generally low, the sand being drab or grey in hue with occasional shells or shell-fragments, but inland it forms hills rising to 300 or even up to 400 ft. over the sea-level, and is grey, chocolate, or deep or even bright red in colour. Where the larger rivers pass through the littoral zone such sand is generally missing on the sides of the main valley.

One of the peculiarities of the coastal belt, namely, the lagoon-like termination of the rivers, has resulted from a recent downward movement of the continent by which the mouths of the rivers have become "drowned"; this subsidence probably exceeded 150 ft. Following thereon the submerged river-mouths, along with their smaller side-streams, have become silted-up, thereby producing embayed alluvial flats bounded by abruptly rising hills, while the main stream feeds a lagoon nearly or entirely cut off from the ocean by a bush-covered sand-spit. In the majority of instances the spit has grown out from the north-eastern side of the valley and terminates opposite a reef of rock that forms the south-eastern side.

This silting-up action along the depressed shore-line has

operated on a larger scale between the Amanzimtoti and the Umgeni rivers, whereby a wide alluvial flat, showing relics of river-terraces, has been produced, cut off from the ocean by sand dunes and by the consolidated calcareous sands of the Bluff; within this tract lies Durban harbour.

Coming to the more detailed geology of the coastal belt, the distribution of the four principal formations is briefly as follows: From just north of the Umtamvuna River granite is the prevailing rock with the Table Mountain Sandstone building the 1300–1600 ft. plateau of the Murchison Flats a short distance inland. Port Shepstone stands on one side of a down-faulted basin, in the heart of which (just north of the Umzimkulu River) is preserved a small area of Ecce “Coal Measures” with Ecce Shales and Dwyka Conglomerate in succession appearing to north-east and south-west, while the palæozoic sandstones become in turn exposed south of Izotsha, where they make a plateau several miles in breadth with an escarpment facing inland. The granite and gneiss continue northwards in a broad belt with a number of Table Mountain Sandstone outliers along the coast, the majority of which are bounded in a northerly direction by faults trending north-eastwards and running obliquely out to sea. The largest of these builds a fairly even plateau just south of the Umtwalumi River sloping seawards and with its inner edge rising to 920 ft. This is continued to Isizela by a more dissected and somewhat treeless slope of Dwyka Conglomerate. Just south of the Umzinto River there is a small area of this sandstone, while a larger one extends thence to Scottsburg, in each case forming exceptionally even park-like country; sandstone outliers cap several ridges around Umzinto. The Dwyka Conglomerate extends from that town northwards in a narrow belt to Durban, with granite and gneiss only a few miles inland and with the Ecce Shales and sometimes even the “Coal Measure” sandstones along the coast; faulting is common. From the Umlazi River northwards the Table Mountain Sandstone generally intervenes between the granite and the Karroo Beds and sometimes covers fairly wide areas as

about Pinetown, but the detailed geology is unknown between this town and the Tongaat River. Anderson's work in Victoria County indicates a somewhat dissected slope rising fairly evenly for some ten or twelve miles inland, whence there is a sudden drop from the Table Mountain Sandstone to the more friable granite. The seaward half of this belt is formed of Karroo Beds, with the Dwyka cropping out inland, followed by the higher horizons near the coast; faulting is not unusual. The "drowning" of the coast is evinced by the broad alluvial belt extending for a number of miles up the valley of the Umvoti River.

II. CLIMATE.

1. TEMPERATURE.

Temperature variations on the coast belt are not extreme as they are at higher altitudes. The average mean temperatures are high and, according to available records, only once—at Stanger in 1893—has the temperature fallen below freezing point; but frosts would probably have been recorded more frequently if observations had been taken continuously at the bottom of any of the valleys. In the early days when sugar-cane cultivation was carried on only on the river flats, injury from frost appears to have been frequently experienced.

The mean amount of cloud over the coast belt is relatively much greater than for the midlands, being 4·7 (if the overcast sky is taken as 10) at Durban, and this leads to a less range of temperatures as a rule, though there are occasionally very high temperatures recorded, e.g. 123° F. for Stanger, where the mean cloudiness is less.

The general absence of frosts, the relatively high mean temperatures and the less range are the chief points which distinguish the coast belt as a whole, and mark it off as distinctly more tropical than any other part of the south-eastern summer-rainfall region of South Africa. The prevailing cloudiness and somewhat high rainfall, which is fairly

evenly distributed, produces a moist heat which is very different in its physiological effects from the dry heat of the main river valleys of Natal.

It is further necessary for our present purpose to examine what differences are shown in the temperature records for different stations on the coast belt. Detailed tables were printed in the first paper of this series¹ and need not be repeated. The different stations will be considered in order from the southern end of the coast belt to the north.

First of all, at Port Shepstone, near the border of East Pondoland (Cape Colony), which is situated on the coast and fully exposed, the average mean maximum is 78.4°F . and the average mean minimum 59° , the average absolute maximum 96.5° and the average absolute minimum 44° . The average greatest range here is 52.5° . The sea breezes temper the extreme heat and the station is furthest away from the tropics line.

The next station is Umzinto, situated about seven miles from the sea in a hot valley. The average mean maximum is 81.6° or 3.2° more than at Port Shepstone; the average mean minimum is 56.2° or 2.8° less than at Port Shepstone. The average absolute maximum is 101° and the average absolute minimum 43° , giving a range of 58° as compared with 52.5° for Port Shepstone. This comparison shows that the valley type of climate can, to a certain extent, be distinguished on the coast belt as well as in the midlands.

For Durban, which is situated about half-way between the Cape Colony border and Zululand, on the coast, the fullest records are available. The following are the averages: Mean, 9 a.m., 69.9° ; mean, 3 p.m., 73.2° ; mean maximum, 79.2° ; mean minimum, 61.5° ; absolute maximum, 98.9° ; absolute minimum, 45.6° ; absolute maximum in sun, 156.1° ; absolute minimum in sun, 129.7° ; mean amount of cloud, 9 a.m., 4.5; 3 p.m., 4.7; overcast sky being taken as 10. The mean maximum is only 1.5° higher, and the mean

¹ Bews, J. W., "The Vegetation of Natal," 'Annals of Natal Museum,' vol. ii, pt. 3, 1912.

minimum 2.5° higher than at Port Shepstone, and the average range is 53.3° as compared with 52.6° for Port Shepstone. Both stations are near the sea and the climates are very similar.

The next station is Verulam, about twenty miles north of Durban and five miles from the sea. The averages here are—mean maximum, 83.3° ; mean minimum, 60.6° ; absolute maximum, 107° ; absolute minimum, 40° . It is hotter than Durban or Umzinto by several degrees, but the average absolute minimum drops to 40° , so that in winter it may be colder. The average range is 67° as compared with 58° for Umzinto, 53.3° for Durban and 52.6° for Port Shepstone. The comparison here given is of considerable interest, for at Verulam the more xerophytic types of vegetation, thornveld and thorn scrub begin to dominate and continue to do so, with euphorbias at intervals in the drier more exposed parts, to the borders of Zululand and beyond.

The last station is Stanger, fifty-two miles north of Durban, seventeen miles south of the Tugela and about five miles from the sea. The averages are: mean maximum, 81.2° ; mean minimum, 59.4° ; absolute maximum, 110° ; absolute minimum, 42° ; range, 68° . This is of the same type as Verulam, the differences being only slight. Both places are very hot with occasionally low temperatures and even frosts in winter; 30° , as already stated, has been recorded for Stanger.

To summarise, stations near the sea show that the heat is tempered by the sea breezes during the day and in summer, while at night and in winter the temperature does not fall very low. On the other hand, stations away from the sea, especially in the valleys, show a greater range of temperatures, being hotter in summer and during the day and often colder in winter or during the night. The temperatures at Port Shepstone and at Durban show little difference, being only slightly hotter at the latter place, but north of Durban, at Verulam and at Stanger, the temperatures are several degrees higher on the average, with lower absolute minima in winter and a considerably greater range.

2. HUMIDITY AND PRECIPITATION.

It is unfortunate that no reliable figures for the relative humidity at different stations are available. It is undoubtedly uniformly high for practically the whole coast belt, as is shown by the successful cultivation of the sugar-cane everywhere. It appears to vary in a manner parallel to the temperature variations, the stations which show a greater range of temperatures also showing lower relative humidity and less cloudiness. Even the rainfall records are not so satisfactory as they might be, there being frequent gaps in the returns for all the stations except Durban.

The average annual rainfall in inches and the average number of days in the year on which rain falls are as follows for the various stations :

	Inches.	Wet days
Port Shepstone (on the coast and fully exposed)	48·19	122
Umzinto (7 miles inland in a valley)	37·69	90
Winkle Spruit (on the coast)	45·67	117
Durban (on the coast)	39·7	137
Verulam (5 miles inland)	38·81	111
Stanger (5 miles inland)	39·94	167

The stations are again arranged in order from south to north. Port Shepstone shows the highest rainfall. It is fully exposed to the rain-bearing winds from the Indian Ocean and a high plateau rises immediately behind it, the coast belt being narrower at this point than anywhere to the north. Umzinto shows the lowest average rainfall. Being a few miles inland and in a valley it is sheltered behind the rising land which lies between it and the coast line. It is therefore drier and, as explained above, it is also hotter, i.e. it begins to show the dry, hot valley-type of climate, though not to the same extent as in the midlands. Durban and the North Coast stations show only slight differences in rainfall, but Stanger is wetter than Verulam and has the rainfall better distributed (167 wet days as against 111).

The distribution of the rainfall over the year is similar for all the stations on the coast belt. At Durban, where the records are available over the longest period, with a total of 39·71 in., the distribution is as follows :

January	. 4·36	May	. . 2·00	September	. 4·18
February	. 4·61	June	. . 0·82	October	. 5·03
March	. 4·69	July	. . 0·79	November	. 4·26
April	. 3·18	August	. 1·37	December	. 4·42

During the three months of winter—June, July and August—only 2·98 in. or 7·5 per cent. of the total falls, or, if we include May, the winter rainfall is, on an average, less than 5 in., or one-eighth of the total amount. Nevertheless, even the driest months, June and July, are seldom without one or two wet days, and although the total winter rainfall is very small in amount, the relative humidity remains fairly high, and seeing that the dry winter season is also free from frosts, the vegetation on the coast belt does not suffer to any extent. The climax or sub-climax types, forest and scrub, remain always rather moist, but the thorn veld type is drier in winter, and with the prevailing anti-cyclonic conditions and absence of winds from the sea there is less cloud. Consequently radiation is increased, and from Verulam northwards, where the thorn veld type prevails, the winter temperatures, as already explained, are lower at night. The temperature and moisture factors always tend to interact and influence each other, and all over Natal the drier parts have also the lower winter temperatures.

3. LIGHT.

In midwinter at Durban the sun rises on the shortest day about 6.52 a.m. and sets at 5.4 p.m., giving a length of day of ten hours twelve minutes. In midsummer the sun rises on the longest day about 4.56 a.m. and sets at 6.55 p.m., giving a length of day of almost exactly fourteen hours. Darkness falls quickly after sunset, there being no long twilight. The intensity of the light throughout the day, owing to the

greater general cloudiness, etc., is less than at higher altitudes. The general effects of the greater chemical intensity of sunlight with increasing altitude were described in a former paper.¹ Various species with a wide range, e.g. *Helichrysum adenocarpum*, *Dierama pendula*, *Moræa spathacea*, show remarkable colour changes in their flowers with ascending altitude, passing from white on the coast through pale pink to deep crimson or even purple on the Drakensberg.

Actinometer measurements are constantly being taken in connection with the photographing of the vegetation types. In the early part of the day the atmosphere is often remarkably clear, and the sensitive paper darkens to the normal tint in about two seconds. It is the only satisfactory time, as a rule, for good photographic work. About 10 a.m. the atmosphere becomes more hazy and later the sky may become overcast.

Owing to the prevalent development of scrub and tree-growth generally there is always plenty of shade, except where the ground has been cleared. The lightest shade is shown by the thorn trees (*Acacia* spp.), but even these reduce the amount of light to as little as '02 of the normal at midday when the sun is overhead, though the numerous plants which grow up underneath the pioneer thorn trees get full sunlight earlier or later in the day when the slanting rays penetrate underneath the umbrella-shaped canopy. In dense scrub and forest, where numerous climbing plants assist in closing in the canopy, the shade is often so dense that only cryptogamic species of plants can grow underneath, and regeneration on the floor of the forest ceases until gaps are produced by the death or destruction of some of the dominant trees. But even where Acanthaceous herbs, etc., are found the light intensity may only be '002 of full sunlight. Among the shrubs the Rubiaceous *Psychotria capensis* is one of the deepest shade resisters. I have

¹ Bews, J. W., "The Plant Ecology of the Drakensberg Range," 'Annals of the Natal Museum,' vol. iii, pt. 3, 1917.

gathered it where the light intensity was only '0025 of the normal in the Stella Bush, Durban (see Pl. XXVI, fig. 2). The light requirements of the commoner species is a subject which must command attention as soon as possible.

4. MOVEMENTS OF THE AIR.

The following are the chief winds on the coast belt of Natal:

(a) During the summer months and exceptionally also in winter, cyclones are frequent in the Indian Ocean, generally moving from the north-east and recurving in towards the coast of Natal. While the depression is in the north-east the winds blow from the east over the coast belt and pressure decreases. This east wind does not deposit moisture, though near the coast line it sweeps up salt spray and sand, and its effect on the vegetation is often very great, as is illustrated in Pl. XXIV, fig. 2, where the *umDoni* (*Eugenia cordata*) is shown greatly deformed, being blown over to the west. The effect of this east wind is seen more markedly on the coast south of Durban than on the north coast, since the cyclonic depression usually recurves in towards the coast about the latitude of Durban. As the depression advances over the coast belt the heat often becomes intense.

(b) When pressure begins to increase the wind goes round to the south-west and the change usually brings heavy rains. This south or south-west wind is the chief rain-bearing wind over the coast belt, but the causes which bring rain further inland are more obscure. The heaviest deposition takes place at the stations near the coast and decreases slightly at the stations further away from the sea. The rain-bearing southerly winds do not affect the vegetation adversely.

(c) Owing to the land heating up faster during the day and the air consequently rising, a sea-breeze blows regularly in the afternoons. It has the effect of tempering the heat and consequently it influences the vegetation, especially near the sea, where it is most felt. The corresponding land-breeze

blows from the land in the early morning, being due to the land cooling down faster at night. Such land- and sea-breezes are too well known to need further description. They occur throughout the year except when they are obscured by the stronger easterly or southerly winds already described.

(d) During the winter months anticyclonic conditions generally prevail over Natal. The high pressure brings cold nights, and with a still atmosphere cold air drainage down the valleys at night is a regular phenomenon. Actual frosts, as already pointed out, are rare, and cold valley mists are not a regular occurrence during winter nights on the coast belt as they are in the midlands. Nevertheless, since the vegetation is so much more tropical on the coast belt, cold air drainage at night is a factor of considerable importance. The cold air flows down the valley like a river and often its upper limits are very sharply defined. As one descends a valley at night one plunges into it suddenly. The plants at a certain level may have to endure temperatures several degrees lower than those a few yards higher up.

(e) Föhn Winds.—These are the dry hot winds of Natal. They are most frequent in autumn as the anticyclonic conditions disappear and cyclones occur more frequently off the coast. The air is drawn out from the mouths of the valleys and the air from above descends to take its place. Being warmed by compression it becomes hotter and hotter the deeper the valley. Föhn winds are most pronounced over the deep valleys of the midlands. They occur only occasionally over the south coast, but they are more frequent over the north coast opposite the great river valleys of the Umvoti and Tugela. As already pointed out the cyclones generally move from the north-east and recurve in towards Durban. On the south coast they push over the land of the coast belt and pressure decreases. This probably explains why "hot winds" are infrequent on the south coast. It is difficult to over-estimate the effect of these dry, hot winds. They are probably of the utmost importance in determining the distribution of thorn veld and thorn scrub, which are common

on the north coast from Verulam northwards, but do not occur on the south coast, being replaced there by more mesophytic types of tree veld, which progress towards mesophytic scrub and forest.

III. FLORISTIC ANALYSIS.

In his "Sketch of the Floral Regions of South Africa," Bolus¹ includes the coast belt of Natal in his south-eastern floral region, a large geographical area comprising the whole eastern side of South Africa. While such a large region is homogeneous to a certain extent, and in particular is distinguished by having a summer rainfall, yet there is considerable diversity in many of the climatic factors. Phillips² has brought forward reasons why the "Eastern Mountain region," consisting of the Drakensberg range, Basutoland, etc., should be separated both from the "South-eastern" and "Kalahari" floral regions as defined by Bolus. Marloth,³ without entering into details, has mapped off a "South-eastern Coast Belt." Ecologically the climates of the great river valleys contrast very strongly with those of the surrounding hills and ridges, and the difference is reflected in the floristic composition of the vegetation, though not to an extent sufficient to distinguish "floral regions."

The climate of the Natal coast belt, as already explained, is far more tropical than that of the rest of the South-eastern region, there being a high average mean temperature, an almost total absence of frost, and a fairly high relative humidity throughout the year. The vegetation has a very distinct tropical physiognomy, as is disclosed by the most superficial examination. It is seen particularly in the sub-climax and climax types of vegetation, the scrub and forest, the mangrove vegetation, the common weeds, and in

¹ Bolus, H., 'Science in South Africa,' 1905.

² Phillips, E. P., "A Contribution to the Flora of the Leribe Plateau and Environs," 'Annals of the South African Museum,' 1917.

³ Marloth, R., 'Report of Brit. Assoc. for Adv. of Science,' Capetown, 1905.

the strand plants. The growth-forms of the component species, the extraordinary abundance of climbing plants, the characters of the foliage and many other features which will be described in detail later, all reflect the tropical nature of the vegetation.

More detailed investigation discloses the fact that the majority of the component species either actually extend northwards through the tropics or have close tropical affinities. About 84 per cent. of the genera and 36 per cent. of the species are recorded in the 'Flora of Tropical Africa'; but if that publication were brought up to date, according to present information, the percentage of tropical species would certainly be found to be even greater. An analysis of the flora of the coast belt from this standpoint is given in the following table:

TABLE I.—Natal Coast Belt.

Genera and species.	Dicotyledons.	Monocotyledons.	Total.
Coast belt genera	480	140	620
Tropical coast belt genera .	395	125	520
Percentage of tropical genera	82·3	89·3	83·9
Coast belt species	1085	415	1500
Tropical coast belt species .	370	175	545
Percentage of tropical species	34·1	42·2	36·3

Doubtful records have been neglected and the total number of species is almost certainly more than 1500. It would appear at the outset, both from the purely ecological and from the floristic standpoints, that there are good reasons why the coast belt of Natal should be considered as part of a distinct subtropical region which would include this portion of Bolus' south-eastern region and also much of his Kalahari region—the subtropical parts of the Transvaal. To test this possibility more fully a further detailed analysis of the separate families has been made on the lines adopted by Bolus. It is set forth in Table II. The percentage of tropical species in each family is also given.

TABLE II.—Natal Coast Belt.

Family.	No. of species.	Percentage of the whole.	Tropical species.	Percentage of tropical species.
1. Leguminosæ . . .	150	10·0	60	40
2. Gramineæ . . .	124	8·3	70	56
3. Compositæ . . .	116	7·7	36	31
4. Cyperaceæ . . .	80	5·3	55	69
5. Acanthaceæ . . .	63	4·2	27	43
6. Orchidaceæ . . .	62	4·1	9	14
7. Asclepiadaceæ . . .	51	3·4	12	23
8. Liliaceæ . . .	50	3·3	11	22
9. Euphorbiaceæ . . .	46	3·1	15	33
10. Rubiaceæ . . .	45	3·0	14	31
11. Labiata . . .	36	2·4	13	36
12. Scrophulariaceæ . . .	34	2·3	15	44
13. Convolvulaceæ . . .	25	1·7	20	80
14. Cucurbitaceæ . . .	22	1·5	11	50
15. Malvaceæ . . .	21	1·4	9	43
16. Iridaceæ . . .	21	1·4	4	19
17. Amaryllidaceæ . . .	21	1·4	4	19
18. Celastrineæ . . .	16	1·1	3	19
19. Anacardiaceæ . . .	15	1·0	4	27
20. Amarantaceæ . . .	15	1·0	11	73
21. Urticaceæ . . .	15	1·0	9	60
22. Solanaceæ . . .	15	1·0	10	67

The other families are arranged in the following order according to the number of species in each: Ampelideæ (14); Bixineæ, Crassulaceæ, Campanulaceæ, Verbenaceæ, Loranthaceæ, Commelinaceæ (12); Caparideæ, Polygalaceæ, Sapindaceæ, Umbelliferæ, Thymeliaceæ, Naiadaceæ (11); Geraniaceæ, Sapotaceæ (10); Apocynaceæ, Gentianaceæ, Polygonaceæ (9); Cruciferæ, Tiliaceæ, Loganiaceæ (8); Rutaceæ, Meliaceæ, Myrtaceæ, Ebenaceæ, Lentibulariaceæ, Dioscoraceæ (7); Caryophyllaceæ, Sterculiaceæ, Rosaceæ, Combretaceæ, Onagrariæ, Araliaceæ, Oleaceæ (6); Rhamneæ, Chenopodiaceæ, Juncaceæ (5); Ranunculaceæ, Anonaceæ, Menispermaceæ, Violaceæ, Portulacaceæ, Lineæ, Rhizophoreæ, Melastomaceæ, Lythariæ, Aizoaceæ, Selagineæ,

Santalaceæ, Cycadaceæ, Aroideæ, Eriocaulæ (4); Passifloraceæ, Primulaceæ, Myrsineæ, Boragineæ, Xyridaceæ (3); Papaveraceæ, Hypericineæ, Malpighiaceæ, Ochnaceæ, Burseraceæ, Olacineæ, Halorageæ, Samydaceæ, Begoniaceæ, Ericaceæ, Gesneraceæ, Pedalineæ, Nyctagineæ, Illecebraceæ, Phytolaccaceæ, Piperaceæ, Laurineæ, Proteaceæ, Scitamineæ, Palmaceæ, Typhaceæ, Lemnaceæ (2); Nymphæaceæ, Pittosporeæ, Guttiferæ, Connaraceæ, Saxifragaceæ, Droseraceæ, Valerianaceæ, Dipsaceæ, Goodenovieæ, Plumbagineæ, Bignoniaceæ, Plantagineæ, Podostemaceæ, Myricaceæ, Ceratophylleæ, Hæmodoraceæ, Flagellariæ (1).

The Leguminosæ and Gramineæ are both better represented than the Compositæ, which, as compared with other parts of South Africa, are relatively scarce. The Leguminosæ, Gramineæ, Cyperaceæ, Acanthaceæ, Euphorbiaceæ, Rubiaceæ, Scrophulariaceæ, Labiataæ, Convolvulaceæ, Cucurbitaceæ, climbing Asclepiadaceæ, Malvaceæ, Amarantaceæ, Urticaceæ, Solanaceæ, Verbenaceæ, Bixineæ, Anonaceæ, Cappari-
daceæ, all show remarkable tropical affinities.

Many families well represented in the midlands of Natal are poorly represented on the coast, e.g. Sterculiaceæ, Geraniaceæ, Umbelliferæ, Campanulaceæ, Crassulaceæ, Ericacæ. The largest coast belt genera are among Dicotyledons: Indigofera, Ipomæa, Senecio, Rhynchosia, Vitis, Vernonia, Euphorbia, Helichrysum, Solanum, Hibiscus, Rhus, Plectranthus, Justicia, Thunbergia, Polygala, Celastrus, Utricularia; and among Monocotyledons: Panicum, Eragrostis, Andropogon, Cyperus, Mariscus, Kyllinga, Digitaria, Eulophia, Habenaria, Asparagus, Commelina, Kniphofia, Aloe.

For the purposes of comparison Bolus' analysis of the chief families with 4764 species belonging to the south-eastern region as a whole is given in Table III.

TABLE III.—South-eastern Region.

Family.	No. of species.	Percentage of the whole.	Family.	No. of species.	Percentage of the whole.
1. Compositæ .	633	13·3	13. Crassulaceæ .	104	2·2
2. Leguminosæ .	400	8·4	14. Euphorbiaceæ .	91	1·9
3. Liliaceæ .	363	7·6	15. Cyperaceæ .	88	1·8
4. Gramineæ .	251	5·3	16. Aizoaceæ .	85	1·8
5. Asclepiadaceæ .	195	4·0	17. Geraniaceæ .	76	1·6
6. Orchidaceæ .	182	3·8	18. Campanulaceæ .	68	1·4
7. Scrophulariaceæ	163	3·4	19. Selaginæ .	61	1·3
8. Iridaceæ .	140	2·9	20. Sterculiaceæ .	56	1·2
9. Acanthaceæ .	122	2·6	21. Convolvulaceæ .	55	1·2
10. Rubiaceæ .	114	2·4	22. Umbelliferæ .	52	1·0
11. Labiataæ .	111	2·3	23. Anacardiaceæ .	48	1·0
12. Amaryllidaceæ .	106	2·2			

It must be kept in mind that the Natal coast belt is included in this analysis by Bolus, and a great many species of such orders as Acanthaceæ, Gramineæ, Euphorbiaceæ, Rubiaceæ, Leguminosæ are confined to the Natal coast belt, so far as South Africa is concerned. If the coast belt were excluded, the difference between it and the rest of the south-eastern region would be seen to be much greater. As it is, the differences in position of such families as Compositæ, Acanthaceæ, Crassulaceæ, Sterculiaceæ, Aizoaceæ, Iridaceæ, Urticaceæ, etc., in the two lists are sufficiently striking. At the same time, of course, the whole south-eastern region partakes of the subtropical character of the coast belt. The midlands of Natal have much in common with the coast belt, the mountain ranges not so much.

IV. SUCCESSIONAL TENDENCIES.

When we investigate the floristic composition in relation to the different stages of the plant succession, certain very interesting facts are brought to light. In some of the earlier stages the edaphic conditions are more important than the climatic. Water and marsh plants commonly have

a wide distribution, and the corresponding plant communities differ but little with considerable climatic variations. The Cyperaceæ and other marsh and water plants include a great many species that extend through the tropics, but the same species also extend through the rest of Natal with a few exceptions. In the same way, many of the strand plants have a wide distribution and extend through the tropics not only of Africa but of Asia as well—and even South America. Ruderal species growing in constantly disturbed habitats are distinctly tropical on the whole, but these are mixed with many that are just as distinctly temperate and range all over South Africa.

In the main xerosere the vegetation becomes distinctly more and more tropical in its physiognomy and floristic composition as succession advances. The earliest stages include species belonging to the Crassulaceæ, Aizoaceæ (e.g. *Limeum viscosum*), *Selaginella rupestris* and several others, which represent a type much more characteristic of the midlands of Natal and other colder parts of South Africa. Primitive grassveld dominated by species of *Aristida*, *Eragrostis*, *Sporobolus*, etc., is practically identical with the same type in the midlands. Even at a further stage of the succession *Anthistiria imberbis* is again dominant on the coast belt, as it is over most of the rest of the south-eastern grassveld. In the numerous vernal aspect socies so abundant in the grassveld the same affinity with the corresponding midland types is seen. Bulbous Monocotyledons, Compositæ, Leguminosæ, Scrophulariaceæ, etc., and a fair number of distinctly temperate species are common. It is interesting, too, to compare the grassveld species of *Asclepiadaceæ*, which all belong to genera much better represented in other parts of South Africa, with the climbing species of the same family found in the coast belt scrub and forest which are distinctly tropical.

As the climax stages of the succession are reached the vegetation becomes much more tropical. Among the trees

and shrubs and innumerable climbers there are two or three hundred tropical species. Only a few of the main families need be mentioned, e.g. Anonaceæ, Menispermaceæ, Capparideæ, Bixineæ, Malvaceæ, Sapindaceæ, Celastrineæ, Leguminosæ, Combretaceæ, Cucurbitaceæ, Rubiaceæ, Sapotaceæ, Apocynaceæ, Convolvulaceæ, Verbenaceæ, Euphorbiaceæ, Urticaceæ, Palmæ. The herbs and undershrubs are also largely tropical, the Acanthaceæ, Labiataæ, Commelinaceæ, Amarantaceæ, Euphorbiaceæ, Leguminosæ and Compositæ being well-represented. Among the grasses the numerous tropical or endemic species of *Panicum*, which are very common around the margin of the scrub, contrast sharply with the earlier grassveld species.

For further information the list of species described under coast scrub should be consulted and attention given to the relative frequency of each species. A careful study of all the facts, only the barest outline of which has been given above, has led to the conclusion that the following may probably be added to the "Laws of Succession" as formulated by Clements.¹

In a subtropical region, as the succession advances, the vegetation becomes more and more tropical.

At present it is perhaps better to regard this as an hypothesis which should be more fully tested in other subtropical regions.

Another general tendency is that widely distributed species usually act as pioneers, or are found in an early stage of the succession. There are, however, exceptions to this, especially in the case of species which are controlled more by edaphic than climatic conditions. Nevertheless, it is particularly true with regard to the majority of the species which have a wide distribution over South Africa. Light-demanding, xerophytic pioneers are able to spread over the drier regions

¹ Clements, F. E., 'Research Methods in Ecology,' Lincoln (Nebraska), 1905.

where more shade-loving, mesophytic species, that in moister places follow them and kill them out, are not able to do so. The recognition of this fact appears to be of the utmost importance in any analysis of the distribution of plants over South Africa generally, but since it does not apply only to the Natal coast belt, a full discussion of details is reserved for a future paper. It may, however, be pointed out here that in a continental area like South Africa, with its great variations in climate, the underlying principles of plant succession probably have far more to do with determining the area occupied by species than the mere age of the species, as postulated by Willis.¹

V. THE PLANT COMMUNITIES.

The different types of plant community will be dealt with in the order of the plant succession, the initial or relatively primitive types being considered first, then the semi-stable intermediate or transitional types, and finally the climax associations. As has been pointed out elsewhere,² it is doubtful whether any of the coast grassveld can be considered a climax type. It seems to be everywhere unstable, and merely a stage in the succession to scrub or forest. At most it may be considered as semi-stable or sub-climax. The only true climax types are the psammophilous bush, which clothes the line of fixed sand-dunes close to the seashore, the coast forest, which occurs behind the dunes on the rest of the coast belt, and a xerophytic thorny scrub, which is found in the drier, hotter localities. It must remain a matter of opinion whether even the first two types should be kept distinct, or whether the associations composing them should be grouped together in the same formation. A very large number of species, including those that are sometimes

¹ Willis, J. C., "The Endemic Flora of Ceylon, with Reference to Geographical Distribution and Evolution in General," 'Phil. Trans.,' B, vol. cxi, 1915. "The Evolution of Species in Ceylon, with Reference to the Dying Out of Species," 'Ann. of Botany,' vol. xxx, 1916.

² Bews, J. W., 'The Grasses and Grasslands of South Africa,' Pietermaritzburg, 1918.

dominant over small areas—i.e. those forming definite societies or small associations—are common to both. As is illustrated diagrammatically in text-fig. 4, the main seres lead up to forest of one kind or another, and consequently most of the coast belt vegetation might be considered as one plant formation. The climate of the coast belt is sufficiently uniform to permit of this view with the exception of the portions where thorn veld is developed, with species of *Acacia* dominant. Though isolated thorn trees occur at various places on the south coast, true thorn veld only becomes a dominant type from Verulam northwards where the climate is drier and hotter. In the midlands thorn veld and thorn scrub fill the river valleys, while forest clothes the south-eastern slopes of the hills above. On the coast belt the position is reversed, the mesophytic or hygrophilous forest occurring in the sheltered valleys, while thorn veld is found on the more exposed and drier ridges. With slightly moister conditions, however, the same class of thorny scrub (e.g. in Zululand beyond the umFolosi and St. Lucia Bay) can be seen to be a stage in the succession to forest, to which it readily gives way. Tree veld progresses towards scrub by the clumps of trees growing closer and closer together. The mangrove type has many of the appearances of stability, but as the mud-level is raised and the water ceases to be brackish—to a large extent a direct effect of the vegetation itself—the mangroves give way immediately to other trees of the scrub or forest. There is no intermingling in this case.

Since many of the common coast species have been illustrated by Medley Wood in his 'Natal Plants,' and for some time to come the identification of South African plants must remain a matter of difficulty, it has been thought useful to indicate in the following pages those species thus illustrated by giving the number of the plate after the names.

1. THE STRAND VEGETATION.

(The initial stages of the psammosere, Pl. XXII, fig. 1.)

On the belt of shifting sand between the sea and the line

of fixed sand-dunes the following species form extensive colonies, consocieties or associates. Most of them are wide-spread strand plants of tropical and sub-tropical regions and such are most abundant. The subordinate species are more often endemic or at any rate restricted in their distribution.

(a) *Hydrophylax carnosus* (Rubiaceæ) (text-fig. 1, A).—This plant is abundant right along the coast. At certain places, e. g. Amanzimtoti, Umgababa, Umhloti, etc., it forms pure consocieties close to the sea, its fleshy, horizontal creeping stems covering long stretches of the sandy beach (Pl. XXII, fig. 1).

(b) *Scævola lobelia* (Goodenovieæ) (text-fig. 1, B).—At Amanzimtoti this species is dominant behind and above the *Hydrophylax*. Elsewhere, e. g. north of Durban, it is dominant near the water and sometimes becomes submerged at high tides. It has thick, fleshy leaves and long rhizomes which creep through the sand, only the leaf-bearing shoots appearing above it (Pl. XXII, fig. 2). *Cyperus natalensis* is often associated with it, travelling for long distances through the sand.

(c) *Ipomæa pes-capræ* (I. *biloba*) (text-fig. 1, C).—This species prefers to creep over the sand, but it often becomes buried where the sand is drifting. It occurs all along the coast, being a very common tropical strand plant, the ecology of which has been dealt with by Schimper.¹ *Ipomæa* consocieties usually stand considerably higher on the beach than the *Hydrophylax* or *Scævola* types (Pl. XXII, fig. 1).

(d) *Mesembryanthemum edule*.—It forms a dense, succulent covering over the surface of the partially fixed sand near the margin of the zone of halophytic shrubs and herbs, which is transitional to the psammophilous bush. It is one of the most important sand-fixing species.

(e) *Sporobolus pungens*.—This widely-distributed sea-shore grass forms dense consocieties and gathers soil so as to produce hard flat mounds in the transitional belt or even

¹ Schimper, A. F. W., 'Die indo-malayische strandflora,' 1891.



TEXT-FIG. 1.—A. *Hydrophylax carnososa* Soud. B. *Scavola lobelia* Morr. C. *Ipomaea biloba* Forsk.

within reach of the spray. It occurs, however, usually not on the more exposed portions of the beach where there are long stretches of sand, but rather in more sheltered places, or among the few isolated patches of rock or near the river-mouths, where the soil is sandy.

(f) *Stenotaphrum glabrum*.—This is a very common seashore grass, and its prostrate rooting stems soon form a close carpet over any bare stretches of sand or sandy soil where the soil-water is not salt. It is not confined to the beach, for it often extends through the open spaces and along the foot-paths in the psammophilous bush. It also occurs frequently in sandy soil behind the dunes and further inland. It is largely used for making lawns.

(g) *Dactyloctenium ægyptiacum*.—Another grass very similar in its growth-form, mode of occurrence and general ecological behaviour to the *Stenotaphrum*. The two last-mentioned grasses are often associated to form a single associates.

(h) All the above form consocieties or associates. Mixed with them there is a considerable variety of other species, some of which form small clumps or societies, all of them being of a halophytic character (Pl. XXII, fig. 2). The Compositæ are represented by *Cryptostemma niveum*, *Brachylaena discolor*, *Osteospermum moniliferum*, *Dimorphotheca fruticosa* (581), *Helichrysum teretifolium*, *Gazania uniflora*, *Berkheya maritima*, *Othonna carnosa* var. *discoidea*, *Launæa bellidifolia*.

Near the upper transitional margin the following grasses occur: *Panicum maximum*, *P. meyerianum*, *P. zizanioides*, and sometimes other species of *Panicum*; *Ehrharta calycina* and *E. erecta* (both common); *Eleusine indica*, *Sporobolus indicus*, *Eragrostis curvula*, *E. plana*, with several other common ruderal species. The Asclepiadaceæ have *Schizoglossum euphorbioides* and the climbing species *Cynanchum obtusifolium* (common), with *C. capense* and *C. natalitium* (rarer). The Leguminosæ are represented by *Tephrosia canescens*, *Cana-*

valia bonariensis and *C. obtusifolia*. Other typical widely-scattered coast halophytes are *Passerina rigida*, *Asparagus sprengeri*, *Chironia baccifera*, *Disperis stenoglossa*, *Acidanthera brevicollis*, *Euphorbia livida*, *Carissa grandiflora*, *Heliophila scandens*, *Peucedanum connatum*, *Hyobanche* sp., and the almost leafless Primulaceous plant, *Samolus porosus*. As those species become more abundant the taller-growing shrubs among them (e. g. *Osteospermum*) tend to exclude the herbaceous forms by shading them, and the type becomes transitional to psammophilous scrub—a stage of the succession which will be dealt with later.

Though there are no stretches of beach-gravel, the belt of shifting sand is interrupted here and there by rocks. In such situations there is little or no change in the vegetation. On the rocks at Isipingo the plants gathered were the following: *Gazania uniflora*, *Dimorphotheca fruticosa*, *Passerina filiformis*, *Helichrysum teretifolium*, *Carissa grandiflora* and a species of *Salicornia*, all of them, except perhaps the last mentioned, typical plants of the sandy seashore.

2. THE LAGOON VEGETATION.

(The initial stages of the halosere, Pl. XXV, fig. 1.)

It is not always easy to distinguish the halosere, where the soil water is salt or brackish, from the psammosere, where the soil-water is not, at any rate, continuously salt. Most of the sandy beach already dealt with slopes rather steeply from the sand-dunes to the sea, and though the various species grow often within reach of the spray, and may even be submerged at exceptionally high tides, yet the sand through which they grow is kept moist by frequent precipitation and by soakage from behind and the water is not salt. At the river mouths, on the other hand, owing to the subsidence of the coast line, there are often extensive mud-flats, as, for instance, in Durban Bay, where the tide ascends

and the water is salt or brackish. Here the dominant vegetation is composed of mangroves, which, as already mentioned, give way to other trees as soon as the soil-level rises beyond the reach of the salt water. The early stages of the halosere is composed of a few characteristic species, which colonise the mud-flats.

(a) *Salicornia* spp.—*Salicornia herbacea* and other species (e.g. *S. natalensis*) form extensive colonies or consociés.

(b) *Chenolea diffusa*.—This species forms clumps by itself or frequently mixes with the *Salicornia*. On the mud-flats at Congella the vegetation consists chiefly of associates of these two (Pl. XXV, fig. 1). There are a number of species of subordinate importance, e.g. *Scirpus littoralis*, *Triglochin laxiflorum*, *Serpicula repens*, *Chaetacanthus personii*, *Fimbristylis obtusifolia*, and the fern *Acrostichum aureum*. *Zostera nana* is recorded for Natal Bay, but I have not seen it. Various grasses, e.g. *Sporobolus pungens*, *Cynodon dactylon*, come in as soon as the mud-level is raised above the reach of the water.

3. LAKE, VLEI AND STREAMBANK VEGETATION.

(The initial stages of the hydrosere.)

On the low-lying portions of the coast belt behind the dunes, and especially near the river-mouths, there is much marshy ground with numerous pools or small lakes. The water is not, as a rule, salt or brackish. The stream banks must also be included in the same habitat. The term "coast flats," so often used by Medley Wood and others in recording the habitat of species, is generally to be understood as representing marshy ground, though portions of such extensive flats may be dry and bear transitional types of vegetation (grass veld or scrub) representing further stages of succession. Further inland, at slightly higher altitudes, the vleis are smaller, occurring chiefly along the streams, and in these the succession advances very rapidly, as a rule, to bush.

Apart from the purely physical difficulties of investigating the coast marshes, under conditions of usually stifling heat, with swarms of mosquitoes, the plant succession is very easy to follow, since it is clearly marked out by a series of successional zones. It is true that the full succession may be obscured by the frequent omission of certain stages in different localities, owing to abrupt variations in environmental conditions, such as the depth or amount of water. The streams often change their courses, and when the sand bars at the river are periodically cut through the lakes are drained out. The sand-bar slowly re-forms and the water is again dammed back. The drainage alters in consequence of such changes, and there may be correspondingly rapid changes in the vegetation, vlei types giving way to stages which belong to the xerosere, i.e. to grassveld. In addition to this, what may be regarded as the normal succession does not always follow the same course. The purely aquatic stages are followed sometimes by *Phragmites* and *Typha*, sometimes by a mixture of semi-aquatic species, including many of the smaller *Cyperaceæ*, and both these types may be followed by the tall-growing species of *Cyperus* and *Mariscus* or both the *Phragmites*-*Typha* associates, and the semi-aquatics may be omitted and the *Cyperus* zone follow on the submerged and floating aquatic stages. It may be well, therefore, to modify the above statement and say that it is easy to follow the succession in any particular vlei, yet it is more difficult to generalise with regard to the coast hydrosere as a whole.

The stages will be dealt with as far as possible in the order of succession, it being clearly understood that certain stages are more or less of equal rank, as is indicated in the diagram (text-fig. 4).

(a) Submerged Aquatics.—The chief plants belonging to this earliest stage are the *Potamogetons*, the species found on the coast-belt being *P. natans*, *P. lucens*, *P. pusillus*, *P. crispus* and *P. friesii*, but they are not, of course, always wholly submerged. *Ceratophyllum demersum* (551) is another characteristic species.

(b) Floating Aquatics.—These occur in shallower water. *Aponogeton natalense* and *A. spathaceum* var. *juncum* are often dominant. *Nymphaea* sp. (near *madagascarenensis*, fide Medley Wood) is another characteristic species. Species of *Utricularia* are common, *U. foliosa*, *U. exoleta*, *U. stellaris*, *U. prehensilis*, *Jussiaea repens* (*J. fluitans*), *Limnanthemum indicum* (34), *Trapa bispinosa*, *Lemna minor*, *L. gibba*, *Wolffia denticulata* also occur in this zone.

(c) Phragmites or Reed Zone.—*Phragmites communis* (Pl. XXV, fig. 2) lines the river banks for long distances and forms often remarkably pure consocieties, probably because the smaller aquatics cannot survive in the dense shade. The reed zone is not so frequent in the vleis, though it does occur. The Spanish Reed, *Arundo donax*, an introduced species, is found in places. It grows usually taller than the *Phragmites*.

(d) Phragmites—Typha Associates.—*Typha capensis* is frequently associated with *Phragmites*, growing in stagnant pools.

(e) Semi-aquatics.—There are a large number of species which grow close to the margin of the open water. They may be looked on as belonging to the *Phragmites* zone but they are light-demanding species, which do not, to any extent, actually mix with the *Phragmites*. Some of them, especially the smaller *Cyperaceæ*, seem to be rather widely adaptable, and grow also among the vlei grasses at a later stage in the succession. *Juncus lomatophyllus* often forms consocieties and is one of the commonest species in this zone. Species of *Xyris* grow in small tufts—*X. anceps*, *X. umbilonis*, *X. natalensis*. There are several semi-aquatic *Utricularias*, *U. tribracteata*, *U. sandersoni*, *U. livida* and sometimes *U. prehensilis*. The *Eriocaulons* (*E. dregei*, *E. ruhlandi* and *E. woodii*) are common. Other characteristic species are: *Limosella aquatica*, *Mentha aquatica*, *Ilysanthes riparia*, *Nasturtium officinalis* (probably introduced), *Sium thunbergii*,

Drosera burkeana, *Ranunculus pinnatus* and occasionally several other of the species mentioned later as characteristic rather of the zone of vlei grasses. Many of the smaller Cyperaceæ are common near the water edge, e.g. *Kyllinga alba*, *K. erecta*, *K. elatior*, *K. melanosperma*, *K. lehmanni*, *Pycnus mundii*, *P. polystachyus*, *P. oakfortensis*, *P. umbrosus*, *P. elegantulus*, *P. ferrugineus*, *Juncellus lævigatus*, a few species of *Cyperus* and *Mariscus*, *Eleocharis limosa*, *Fimbristylis complanata*, *F. ferruginea*, *F. exilis*, *Bulbostylis cinnamomea*, *B. striatella*, *B. zeyheri*, *Scirpus macer*, *S. prolifer*, *S. rivularis*, *Ficinea laciniata*, *Fuirena ecklonii*, *F. microlepis*, *Lipocarpa argentea*, *Scleria catophylla*, *S. hirtella*, *S. holcoides*, *S. melanophala*, *S. natalensis*, though they are not all confined to this particular habitat or stage in the succession. I have not collected any species of *Carex* on the coast belt.

Some of the semi-aquatic vlei grasses occasionally find a place in this zone, but they rarely dominate at so early a stage of the succession.

(f) *Cyperus-Mariscus* Associates.—A very clearly-marked zone is dominated by tall growing species of *Cyperus* or *Mariscus*. The smaller semi-aquatics are to a large extent crowded out, and there are often fairly large pure consociates of such species as *C. fastigiatus*, *C. latifolius* or *C. distans*. In Zululand the *Papyrus* (*Cyperus papyrus*) is of extreme ecological importance, covering great tracts of swampy ground. It does not occur in Natal, but a smaller *papyrus* (*C. madagascarensis*) is fairly common as far as Port Shepstone and beyond. The other species of the *Cyperus-Mariscus* zone are: *Cyperus sphærospermus*, *C. denudatus*, *C. isocladius*, *C. latifolius*, *C. distans*, *C. corymbosus*, *C. natalensis*, *C. fastigiatus*, *C. immensus*, *Mariscus elatior*, *M. owani*, *M. gueinzii*, *M. elephantinus*, *M. cooperi*, *M. riparius*, *M. umbilensis*, *Rynchospora aurea*, *R. cyperoides*, *Cladium mariscus*.

Wherever open spaces permit, many of the smaller Cyperaceæ already named are mixed with the taller species, and occasionally there are some of the vlei orchids, etc., to be named later.

(g) Vlei Grasses.—In this zone the water may disappear in the dry season, at least from the surface, though the soil remains water-logged at no great depth. In the rainy season the zone becomes flooded at intervals. Extensive consocieties or associates of the following grasses are common: *Leersia hexandra*, *Setaria aurea*, *Eragrostis namaquensis* var. *robusta*, *Imperata arundinacea*, *Setaria nigrirostris*, *S. gerrardi*, *Panicum proliferum* var. *paludosum*, *P. maximum*, *P. crus-pavonis*, *P. æquinerve*, *P. interruptum*, *Polypogon monspeliensis*, *Trichopteryx dregeana*, *Leptocarydion vulpiastrum*, *Ischæmum fasciculatum*, *Rottbœllia compressa* var. *fasciculata*, and in open spaces, *Stenotaphrum glabrum*.

When other species of Gramineæ, such as the Tambookie grasses (tall *Andropogons*), and numerous coast *Panicums* with *Setaria sulcata*, all of which will be dealt with later, become increasingly intermingled with the true vlei grasses, the type becomes transitional to coast scrub or forest.

There are numerous vlei plants associated with the grasses, many of which form vernal or autumnal aspect societies, while others grow rather sparsely scattered. Among these the Orchidaceæ are rather well represented by *Eulophia barbata*, *E. caffra*, *E. purpurascens*, *E. flaccida*, *E. papillosa*, *E. natalensis*, *Lissochilus clitellifer*, *L. buchanani*, *Schizochilus sandersoni*, *Zeuxine cochlearis* (582), *Platylepis australis*, *Habenaria clavata*, *H. ciliosa*, *H. dives*, *H. porrecta*, *H. fulcicornis*, *Satyrion sphaerocarpum*, *S. atherstonei*, *S. aphyllum*, *Disa stachyoides*, *D. polygonoides*, *Disperis cardiophora*, *D. stenoglossa*, *Corycium nigrescens*.

Among the other Monocotyledons there are: *Moræa*
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spathacea, *Gladiolus papilio* (528), *Hesperantha modesta*, *Anoiganthus brevifolius*, *Aristea eckloni* (68), *Cyrtanthus mackenii* (51), *Crinum longifolium*, *Kniphofia pauciflora*, *K. natalensis* (305), *K. rooperi* (540), *Urginea lilacina* (204), *Commelina africana*, *C. nudiflora*, *Coleotrype natalensis* (48), *Aneilema sinicum*, *Floscopa glomerata*.

The Dicotyledons more often grow in small clumps, though some of the species named above also form conspicuous socies. *Gunnera perpensa* (Haloragææ), *uGoba*, is sometimes completely dominant and forms small consocies.

Other characteristic Dicotyledons are: *Ranunculus pinnatus*, *Polygala capillaris* (83), *Hypericum lalandii*, *Pelargonium australe*, *Vigna glabra*, *V. retusa*, *Æschynomene erubescens*, *Drosera burkeana*, *Dissotis eximia*, *D. incana*, *D. phæotricha*, *Lythrum rivulare*, *Epilobium capense*, *Jussiaea suffruticosa*, *Hydrocotyle asiatica*, *Anthospermum lanceolatum*, *Valeriana capensis*, *Adenostemma viscosum* (= *A. caffrum* (346)), *Denekia capensis* (365), *Helichrysum aureo-nitens*, *Pulicaria capensis*, *Leontonyx tomentosus*, *Senecio caudatus*, *S. picridifolius*, *Lobelia decipiens*, *L. stellaroides* (345), *Chironia purpurascens*, *Sopubia simplex* (364), *Bopusia scabra*, *Teucrium riparium*, *Polygonum lanigerum*, *P. lapathifolium*.

Many of these species are found also in the moist transitional zone around the margins of the scrub and bush.

The rest of the hydrosere consists of the following stages:

(h) Tambookie Associes.—*Andropogon* spp., *Panicum* spp., etc.

(i) Hydrophilous Trees and Shrubs.—*Ficus* spp., *Eugenia cordata*, *Voacanga dregei*, *Rauwolfia natalensis*, etc.

(j) Forest.—Since these are part of the final stages or forest sere they will be considered later, in accordance with our scheme of presenting all the primitive types first.

4. GRASSVELD.

(The initial stages of the xerosere.)

The grassveld on the coast belt is relatively not nearly so extensive as in the midlands or mountain regions of Natal or in any other part of the Eastern Grassveld region of South Africa. Such portions of grassveld as do occur are also relatively far more unstable than that of the midlands, giving way everywhere readily to scrub. At the present time this fact is partly obscured owing to both scrub and grassveld areas being planted with sugar-cane all along the coast belt, but there can be no doubt as to the indications in those portions which remain uncultivated. Apart from its relative instability, the grassveld—at least in so far as the commoner grasses are concerned—does not differ very markedly from midland grassveld, though its subtropical nature is shown by the inclusion of a number of tropical or northern Transvaal species, e. g. *Pollinia villosa*, *Pogonarthria falcata*, *Perotis latifolia*, *Andropogon hirtiflorus*.

The chief stages of the succession in the xerosere are as follows :

(a) LITHOPHYTES.—Lichens are relatively quite unimportant. Mosses and hepatics are much more abundant, the following being representative: *Weisia viridula* (L.) *Hedw.*, *W. hypoleuca* *Wag. & Broth.*, *Campylopus nanum* *C. N.*, *Fissidens bryoides* (L.) *Hedw.*, *Bartramidula globosa* (C. N.) *Broth.* (moist rocks); *Macromitrium lycopodioides* (Burch.) *Schw.* and several species of *Brachythecium* and *Rhyncostegium*; also the hepatics *Notoscyphus lutescens* (L. & L.) *Mitt.*, *Blyttia lyelli* *G. & L. & N.* and *Fimbriaria marginata* *Nees*.

Selaginella rupestris is a frequent lithophyte, and in very shallow soil over bare flat rocks there are found several species of *Crassula*, *Cyanotis nodiflora* and small annuals, e. g. *Limeum viscosum*.

(b) CHOMOPHYTES OR CREVICE PLANTS.—Practically any seed may germinate in a rock crevice and the seedling establishes

itself, and grows at least for a time, so that almost the whole flora of a district may be found in the rocky situations. Only a few of the rarer species are, so far as is known, confined to such situations, e. g. *Ilysanthes nana* (597), *Gladiolus saundersii* (342), *Bulbinella carnososa*.

If scrub is well developed around the bare rocky areas, the seeds of the various shrubs and trees arrive first and scrub develops forthwith, grassland as an intermediate stage being omitted. This is what usually happens at the present time, and one cannot but suspect that much of the coast grassveld at present occupies situations where scrub or forest has been destroyed by fire or otherwise. Grassveld also, however, as explained above, by the draining out of vleis replaces vlei vegetation, and in such cases only gradually gives way to scrub. The exact position of grassveld in the prisere is, therefore, not easy to determine. It is certainly more primitive than scrub, to which it naturally gives way. If it replaces scrub it only does so when the scrub has been destroyed completely either by clearing operations or by burning. The succession in the grassveld itself can only be determined by studying subseres, as when the grasses recolonise the numerous abandoned roads, where the vegetation has been trampled out, or, on a larger scale, by noting what happens when the veld has been continuously burned every year for a long period, with the result that primitive types take possession. When the farmer begins to realise that such primitive types, consisting of coarse xerophytic deep-rooted grasses, have little grazing value, and consequently ceases to burn the grass annually, an opportunity is given for observing how the primitive types give way to more advanced stages of the succession.

(c) PRIMITIVE GRASSVELD.—The chief pioneer grasses over most of the coast belt are species of *Eragrostis* (*E. curvula*, *E. plana*, *E. chalcantha*, *E. chloromelas*), and species of *Sporobolus* (*S. indicus*, *S. rehmanni*, *S. centrifugus*). *Cynodon dactylon* frequently colonises open spaces, especially along pathways and abandoned cattle

kraals, etc., but is easily killed out by shading. *Tragus racemosus* and *Crossotropis grandiglumis* grow on dry, bare slopes. On sandy soil the strand grasses *Stenotaphrum glabrum* and *Dactyloctenium ægyptiacum* remain the chief pioneers. The genus *Aristida* is also important as in the midlands and interior generally, and is represented by *A. barbicollis*, *A. junciformis*, *A. bipartita* and *A. angustata*. Along the roadsides there are, of course, many ruderal grasses, but these hardly belong to true primitive grassveld. In primitive grassveld the various vernal aspect species are much more prominent.

(d) GRASSVELD.—This is a semi-stable or subclimax type. The degree of stability which it possesses it owes partly to the fact that grass fires prevent the succession going any further and scrub developing, and partly to the fact that once scrub has been entirely destroyed over a considerable area it takes a fairly long time for seeds to be retransported and for scrub to recolonise. Since the pure grassveld areas on the coast belt are not nearly so extensive as elsewhere in South Africa, and scrub is never very far distant, this probably affords at least a partial explanation of the relative instability of the coast grassveld when compared with that of the midlands of Natal or the highveld of the Transvaal. In the latter case there are enormous areas entirely free from trees of any kind.

The dominant grasses, with few exceptions, are those of the midlands. *Anthistiria imberbis* (*Themeda forskalii*) is dominant over considerable stretches. *Andropogon hirtus* also forms large consocieties. *Pollinia villosa* is common. *Rottbællia compressa*, *Urelytrum squarrosus*, *Andropogon ceresiæformis*, *A. hirtiflorus*, *A. contortus*, *A. schirensis*, *A. eucomus*, *Digitaria eriantha*, *Panicum serratum*, *P. natalense*, *Axonopus semialatus* var. *ecklonii*, *Tricholæna setifolia*, *Trichopteryx simplex*, *Perotis latifolia*, *Pogonarthria falcata*, *Eragrostis brizoides*, *Chloris virgata* are all prominent species.

The absence or extreme rarity of such prominent midland

and mountain genera as *Festuca*, *Poa*, *Microchloa*, *Harpechloa*, *Anthoxanthum*, *Agrostis*, *Avenastrum*, *Brachypodium*, *Kœleria*, *Pentaschistis* and *Danthonia* is worthy of note. The coast belt grasses all belong to tropical tribes, but the most tropical of them are not grassveld species. Although there are a large number of coast belt grasses, comparatively few are found in the grassveld itself. Many are vlei species, many are ruderal, and a still greater number of very distinctive species of grass are found in the moist margin of scrub and forest. Among them all the temperate tribes, such as the *Aveneæ*, *Festuceæ* and *Hordeæ*, are very poorly represented. The few species with temperate affinities which do occur, e. g. *Ehrharta calycina*, *E. erecta*, are sea-shore species, or (e. g. *Bromus unioloides*) are ruderal and have been introduced.

(e) ASPECT SOCIETIES IN THE GRASSVELD.—In addition to the grasses there occur in the grassveld a large number of other species, which, in former papers, were dealt with under the general heading of “associated veld plants.” In the Natal grassveld there are two chief aspects, the vernal and autumnal. The vernal aspect plants are, to a certain extent, “complementary” to the grasses, since they are, as a rule, deeper-rooted, having underground storage organs of one kind or another (bulbs, corms, rhizomes, tubers, tuberous roots). Nevertheless, they are not altogether complementary, for they gradually diminish in numbers and tend to disappear if the grass is left unburnt, or, in other words, the grasses can suppress most of them under natural conditions. The laying bare of the soil in spring by the burning of the grass enables the sun’s rays to heat the soil to a sufficient depth to cause the vernal plants to commence growth before the grasses, which have no underground water storage and have to wait for the spring rains. The various vernal aspect societies spread rapidly on burnt areas. On the other hand, in unburnt areas they cease to be prominent, though they may remain dormant under the soil for several years, as is shown by the fact that where grass has been left unburnt for a

considerable period of years and then is burnt the ground is to be seen again carpeted with a profusion of spring flowers.

The autumnal plants differ from the vernal, not only in being more prominent in autumn, but in entering into more direct competition with the grasses. They are usually shrubby species, which grow as tall as or taller than the grasses. They are not favoured by the burning of the grass, but, on the contrary, tend to be killed out by it, the necessity of killing them being one of the reasons given for the practice of grass burning. The Tambookie associates of grasses (*Andropogon* spp.), in so far as it occurs in the grassveld, may be reckoned as autumnal. All the autumnal aspect plants are similar to the types which are transitional to scrub, with which they might be included.

1. VERNAL ASPECT SPECIES.—The family Leguminosæ includes a large number. Several of them, e. g. the species of *Crotalaria*, are known to be the cause of diseases of stock, and that the spread of such species is shown to be favoured by grass-burning is one of the important economic results of the study of plant ecology in Natal. The following species are common on the coast belt: *Lotononis corymbosa* (235), *L. carinata*, *L. cytisoides*, *L. dichiloides* (509), *Aspalathus spinosa*, *A. laricifolia* (238), *Crotalaria burkeana*, *C. striata* (532), *C. globifera* (234), *C. lanceolata* (291), *C. macrocarpa*, *Argyrolobium rupestre*, *A. longifolium*, *A. uniflorum* (227), *A. stipulaceum* (274), *Trifolium africanum*, *Lotus discolor* (230), *Indigofera fastigiata*, *I. hilaris*, *Tephrosia longipes*, *Æschynomene micrantha*, *Sesbania ægyptiaca*, *Vigna tenuis*, *V. triloba*, *Zornia bracteata*, *Desmodium hirtum* (212), *Pseudarthria hookeri* (219), *Rhynchosia adenodes*, *R. gibba*, *R. hirsuta*, *R. orthodanum* (220), *R. pilosa*, *R. quadrata*, *R. sigmoides*, *R. memnomia* (349), *R. totta*, *Eriosema kraussianum*, *E. parviflorum* (91), *E. salignum* (337).

Of equal importance is the family Compositæ, some of which are again under suspicion of being the cause of stock

diseases. Individually they are even more abundant than the Leguminosæ. *Senecio latifolius* is very abundant in spring, and all the others are common: *Vernonia natalensis* (333), *V. corymbosa*, *V. hirsuta* (335), *V. piniifolia*, *V. kraussii* (334), *V. dregeana* (366), *V. vernonella* (332), *Aster asper* (12), *A. erigeroides*, *Blumea lacera*, *B. natalensis*, *Conyza incisa*, *Helichrysum flanaganii*, *H. cephaloideum*, *H. kraussii* (269), *H. teretifolium* (327), *H. griseum* (549), *H. umbraculigerum*, *Lopholæna dregeana*, *Senecio lasiorhizus*, *S. erubescens*, *S. pterophyllus* var. *apterus*, *S. speciosus* (550), *Othonna natalensis* (64), *Gazania longiscapa* (351), *Dicoma sessiliflora*, *Gerbera kraussii* (56), *G. piloselloides*, *G. tuberosa*, *G. natalensis* (546).

There is a general similarity in growth-form among the majority of the species belonging to both these large families. There is usually a large, woody or somewhat fleshy underground stem, which branches profusely from a surface "crown," the aerial branches being herbaceous or semi-herbaceous. These die back or are burned off each year. The species, therefore, belong to the groups hemicryptophytes or chamæphytes,¹ according to whether the renewal buds are just underneath the surface of the soil or just above it.

Another large class of vernal species is composed of geophytic monocotyledons with tubers, corms and bulbs, many of which occupy a deeper layer of soil.

The Liliaceæ include *Eriospermum junodi*, *E. natalense* (73), *E. ornithogaloïdes*, *Anthericum elongatum* (208), *A. hirsutum*, *A. robustum*, *Chlorophytum longifolium*, *C. comosum* (279), *C. modestum*, *Tulbaghia leucantha*, *Drimiopsis maculata* (304), *Dipcadi umbonatum*, *D. viride* (239), *Scilla lanceæfolia* (202), *S. inandensis*, *Ornithogalum inandense*, *O. virens* (70), *O. graminifolium*, *O. oliganthum*, *Androcymbium decipiens* and *Aloe kraussii* (292).

¹ Bews, J. W., "The Growth-forms of Natal Plants," 'Trans. Roy. Soc. of S. Africa,' 1916.

The Amaryllidaceæ include *Hypoxis filiformis*, *H. rigidula* (552), *H. argentea* var. *sericea*, *H. acuminata*, *H. gerrardi*, *H. junodii*, *H. membranacea*, *H. oligotricha*, *H. woodii*, *Apodolirion ettæ*, *Cyrtanthus angustifolius* (5), *C. sanguineus* (341), *Hæmanthus natalensis* (58), *Buphane disticha* (595).

The Iridaceæ: *Moræa spathacea*, *M. tricuspis*, *Aristea anceps* (558), *A. torulosa*, *A. schizolæna*, *A. eckloni*, *Hesperantha baurii*, *H. lactea*, *Ixia trichorhiza*, *Lapeyrousea cruenta* (54), *Watsonia densiflora*, *Tritonia laxifolia*, *T. lineata*, *Glaadiolus inandensis*.

The Orchidaceæ: *Eulophia æmula*, *E. purpurascens*, *E. hians*, *E. dregeana*, *E. inæqualis*, *Lissochilus æqualis*, *L. streptopetalus*, *L. arenarius*, *Brachycorythis ovata*, *B. pubescens*, *Habenaria foliosa*, *H. dregeana*, *H. porrecta*, *Bonatea boltoni*, *Satyrium macrophyllum*, *Disa extinctoria*, *Disperis cardiophora*.

The Asclepiadaceæ are represented on the coast belt by a large number of climbing species in the scrub. In the grassveld the species which occur are similar to the bulbous monocotyledons in being geophytes often with very large underground tubers. The following are common: *Raphionacme elata*, *R. galpini*, *R. divaricata*, *Xysmalobium involucratum*, *X. orbiculare*, *Periglossum mackenii*, *Schizoglossum virens*, *S. robustum*, *S. tubulosum* (505), *S. carinatum*, *Pachycarpus scaber* (553), *Asclepias præmorsa*, *A. peltigera* (559), *A. flexuosa*, *A. brevicuspis*, *A. albens*, *Sphærocodon obtusifolium*, *Sisyranthès imberbis*, *Brachystelma sandersoni* (511), *Woodia verruculosa* (554).

The Acanthaceæ are also very abundant on the coast belt, but their favourite habitat is the moist margin of the scrub. A few occur in or spread through the grassveld, e. g. *Thunbergia atriplicifolia* (594), *Ruellia ovata*, *Dyschoriste depressa*, *Chætacanthus burchellii*

(213), *C. glandulosus*, *Blepharis pruinosa*, *Crabbea hirsuta*, *Justicia pulegioides* (216).

The Rubiaceæ in Natal are a distinctly forest or scrub family, consisting mostly of shrubs and small trees, but *Oldenlandia* (*Hedyotis*) *amatymbica*, *O. caffra*, *O. macrophylla* (36), *O. decumbens*, *O. chlorophylla*, *Spermacoce natalensis* and *Pentanisia variabilis* (251) are herbaceous and occur in the grassveld.

Similarly the Euphorbiaceæ are mostly found in scrub or forest, but the following are grassveld species: *Euphorbia natalensis* (302), *E. woodii*, *E. inæquilatera*, *E. gueinzii*, *E. striata*, *E. bupleurifolia*, *Acalypha glabrata*, *A. schultzii*, *A. peduncularis*, *Jatropha hirsuta* (71) and often *Cluytia pulchella* (84).

Among the other grassveld vernal species the Labiatae include: *Becium obovatum* (257), *Syncolostemon densiflorus*, *Stachys æthiopica*, *S. nigricans* (271), *S. galpini*, *S. lupulina*. The Thymeliaceæ: *Gnidia ovalifolia* (248), *G. nodiflora*, *Lasiosiphon kraussii* (256), *L. meisnerianus*, *L. splendens*, *L. anthylloides* (270).

The Scrophulariaceæ are represented by *Peliosotomum calycinum*, *Diascia racemulosa*, *Nemesia floribunda*, *Manulea parviflora*, *M. thyrsoiflora* var. *versicolor*, *Sutera kraussiana*, *S. natalensis*, *S. pallescens*, *S. pinnatifida* var. *subcanescens*, *Zaluzianskya maritima*, *Mimulus gracilis*, *Buchnera dura* and the hemiparasites *Striga orobanchoides*, *S. thunbergii*, *Melasma orobanchoides*, *M. melampyroides* (397), *Cycnium adonense* (273), *Rhamphicarpa tubulosa*, *Harveya coccinea*, *H. bolusii*, *H. speciosa*.

The Santalaceæ are also hemiparasites, and are represented by species of *Thesium* (*T. impletum*, *T. gypsophylloides* and others).

There are a few species of *Solanum* in the coast grassveld, e. g. *S. panduræforme* (596), *S. torvum*, *S. aculeatissimum*, *S. bifurcum*.

The Campanulaceæ include *Wahlenbergia undulata* (37), *Cyphia elata*, *Lightfootia corymbosa*, *Roella glomerata* and the Selagineæ, *Hebenstreitia comosa* (67), *H. integrifolia*, *Selago hyssopifolia*.

Other families, chiefly more temperate, which have numerous representatives at higher altitudes, are poorly represented on the coast belt, but the following isolated species occur: *Heliophila linearis*, *H. virgata*, *Polygala hottentotta*, *Ionidium thymifolium*, *I. cafferum*, *Dianthus prostratus*, *Silene thunbergii*, *Hypericum æthiopicum*, *Corchorus trilocularis*, *Oxalis corniculata*, *O. semiloba*, *Geranium ornithopodum*, *Monsonia ovata* (97), *Pelargonium aconitiphyllum* (368), *P. pulverulentum*, *Eugenia albanensis*, *Tryphostemma sandersoni*, *Hermannia sandersoni*, *Hydrocotyle asiatica*, *Peucedanum capense*, *P. cornatum*, *Scabiosa columbaria*, *Sebæa natalensis*, *S. acutiloba*, *Ipomæa plantaginea* (15), *Cynoglossum enerve*, *C. lanceolatum*, *Sericocoma chrysurus*.

Some of the hygrophilous species already named as characteristic of the zone of vlei grasses are fairly adaptable and spread through the grassveld. Among the Cyperaceæ there are a few species which are xerophytic grassveld types, e. g. *Bulbostylis collina*, *B. cardiocarpa*, *Fimbristylis monostachya*, *Ascolepis capensis*. *Cyperus sexangularis* also sometimes forms sociies in the grassveld, but in fairly moist situations.

Most of the vernal aspect species flower early, from August to November, though some of them flower all through the summer, and a few flower late, yet nevertheless are more conspicuous in spring.

2. AUTUMNAL ASPECT SPECIES.—As already remarked, it is somewhat difficult to separate these types from the initial stages of the scrub, and it is open to question whether they ought to be separated. They compete with the grasses, they spread if the grass is not burned, they often grow taller than the grasses and throw a dense shade. They only differ from

the marginal zone of the scrub in being more xerophytic and more intolerant of shade, and although they do occur around the scrub they are not more abundant in that situation than on open grassy hillsides. They are separated from the vernal aspect species by their general growth-form and behaviour, as already described, and also by the fact that they are not more conspicuous in spring, but grow slowly with the grass and flower any time through the summer or autumn.

The Bracken Fern (*Pteris aquilina*) forms very conspicuous and often large pure consocieties. Its dense shade kills out everything else. Slight depressions and incipient dongas often become filled with it. Occasionally, but by no means always, it is marginal to scrub.

Leonotis leonurus (53) (*uMunyani*) is one of the best-known veld shrubs in Natal, being used medicinally by the natives and cultivated in gardens. It forms conspicuous clumps in the grassveld 4-6 ft. high, and occurs also along the margin of the scrub.

Vangueria latifolia (215), *Lippia asperifolia*, *Rhus discolor*, *Athanasia acerosa*, *Artemesia afra*, *Wedelia natalensis* (250), *Callilepis laureola* (62), *Polygala oppositifolia* (398) all form conspicuous autumnal aspect societies.

The following Leguminosæ are more conspicuous in autumn than in spring: *Tephrosia macropoda*, *Crotolaria capensis* (92), *C. natalitia*, *Indigofera arrecta* (287), *I. micrantha* (82), *Desmodium hirtum* (212), *Pseudarthria hookeri* (219), *Calpurnia intrusa*, as are also the following Compositæ: *Nidorella auriculata*, *Cassinia phyllifolia* (355), *Helichrysum cooperi*, *Schistostephium cratægifolium*, *S. rotundifolium*, *S. spp.* (*Tanacetum griseum* and *T. heptalobum*).

It is not always easy to separate the vernal and autumnal aspect species, unless by careful study throughout the year. A very good test seems to be to answer the question, "Does the species tend to spread if the grass is left unburnt?" If it does, then it will be an autumnal aspect species. Or, if

it is preferred, the question may be applied to the vernal species. "Do they tend to increase where the grass is regularly burnt?" The mere time of flowering, as already explained, is no safe guide, and the collectors' notes on species, as a rule, do not help at all.

5. RUDERAL VEGETATION.

(Weeds, etc. The initial stages of subseres.)

Along roadsides and Kafir pathways, in ditches and quarries, on rubbish heaps and waste land or in cultivated fields, there are found a great many ruderal species which are classified from the standpoint of plant succession as the initial stages of subseres. The original vegetation has been destroyed and the soil is disturbed, but as soon as it is left alone, the processes of repair are initiated and the succession progresses back to the original grassveld, scrub or forest. The majority of the ruderal species flower profusely and for a long period each year and form large quantities of seed. Many are annuals (therophytes), especially in cultivated land. These gradually give way to perennials as the succession advances. Many of the perennials have a creeping habit of growth, which renders them very effective colonisers, and also enables them to withstand adverse conditions. Very few of them can withstand shade, and it is their light requirements chiefly which cause them to give way to other species when the habitat ceases to be interfered with.

Most of the ruderals of the coast belt are markedly tropical in their affinities, and many species (e.g. of *Amarantaceæ*, *Euphorbiaceæ*, etc.), which are widely distributed over the tropics, are included. There are, however, also a number of temperate species, mostly introduced.

The family *Amarantaceæ* includes a number of species, all of them very abundant: *Gomphrena globosa* and *Alternanthera achyranthoides* are both very common along roadsides and garden pathways, etc., the former also proving a troublesome weed in lawns. Other common species

are *Amarantus spinosus* (310), *A. græcizans*, *Cyathula cylindrica*, *C. globulifera*, *Celosia trigyna*, *Achyranthes aspera*, *A. alba*, *A. avicularis*, *A. robusta*, *Hermbstædtia caffra*, *Ærva lanata*.

Among the *Polygonaceæ* there are *Emex australis* (360) (Devil's Thorn), *E. spinosa*, *Rumex obtusifolius* and *Polygonum aviculare*, and in the *Illecebraceæ*, two species, *Pollichia campestris* and *Corrigiola littoralis*.

The *Euphorbiaceæ* include certain small annual *Euphorbias* (*E. hirta*, *E. pilulifera* with its variety *procumbens*, *E. sanguinea* with its variety *intermedia*, *E. hypericifolia*, *E. prostrata*, *E. peplus*), all of which are widely distributed over the tropics, as well as *Acalypha eckloni* and *Ricinus communis*.

The *Compositæ* are perhaps not quite so abundant on the coast belt as in the midlands, but more or less the same species are represented with certain additions: e.g. *Eclipta alba*, *Tridax procumbens*, *Spilanthus acmella*, *Siegesbeckia orientalis*, all coast species and *Bidens pilosa*, *Erigeron canadense*, *Xanthium occidentale*, *X. spinosum*, *X. italicum*, *Galinsoga parviflora*, *Cryptostemma calendulaceum*, *Schkuria bonariensis*, *Acanthospermum brazilum*, *Ageratum conyzoides*, *Gnaphalium purpureum*, *Sonchus oleraceus*, *Heli-chrysum foetidum* more widely distributed.

The *Solanaceæ* include a number of very common weeds: *Datura stramonium* (Stinkblaar), *Nicandra physaloides*, *Physalis peruviana* (Cape Gooseberry) and *Solanum nigrum*; while among the *Malvaceæ* are *Malva parviflora*, *Abutilon indicum*, *A. sonneritium*, *Sida rhombifolia*, *S. spinosa*, *S. triloba*, *Hibiscus physaloides* (379), *H. surattensis* (358), *H. trionum*.

Among the large family of the *Leguminosæ* there are only one or two ruderals, e.g. *Lotononis dichiloides* (509) and *Tephrosia grandiflora*.

Belonging to other dicotyledonous families there are:

Argemone mexicana, *Fumaria officinalis*, *Polycarpon tetraphyllum*, *Waltheria indica*, *Portulacca oleracea*, *Anagallis arvensis*, *Wahlenbergia undulata*, *Asclepias physocarpa* (217), *Oxalis corniculata*, *Barleria obtusa*, *Asystasia coromandeliana*, *Lippia asperifolia*, *Lantana camara*, *Verbena officinalis*, *Leucas martinicensis*, *Teucrium riparium*, *Cerathotheca triloba* (367), *Mirabilis jalapa*, *Boerhaavia repens*, *Phytolacca stricta* (3), *P. octandra*, *Chenopodium ambrosoides*, *C. botrys*, *C. murale*, *Cannabis sativa*, *Urtica urens*.

Apart from the grasses, there are not many monocotyledonous weeds, but most of the Commelinaceæ (see under "Scrub") frequently occur as ruderals, and *Cyperus esculentus* is a troublesome weed. *Cyperus albostrigatus* and *Mariscus dregeanus* are common along roadsides.

Finally, there are a large number of ruderal grasses on the coast belt, mostly species once more of distinct tropical affinities: *Digitaria sanguinalis*, *D. ternata*, *D. horizontalis*, *D. debilis*, *D. diversinervis*, *Panicum brizanthum*, *P. trichopus*, *P. crus-pavonis*, *P. filiculme*, *P. hymeniochilum*, *P. æquinerve*, *P. chusqueoides*, *P. zizanioides*, *P. deustum*, *P. maximum*, *P. lævifolium*, *P. meyerianum*, *P. proliferum* var. *longijubatum*, *P. dregeanum*, *P. miliare*, *Setaria imberbis*, *S. sulcata*, *S. nigrirostris*, *S. verticillata*, *Pennisetum unisetum*, *P. typhoideum*, *Tricholæna rosea*, all belong to the tropical tribe of the Paniceæ.

Other common ruderal species of grasses are: *Chloris pycnothrix*, *C. virgata* and *C. gayana*, *Eleusine indica*, *Sporobolus indicus*, *Eragrostis curvula*, *E. plana*, *E. aspera*, *E. annulata*, *E. obtusa*, *E. major*, *Bromus unioloides*, *Lolium temulentum*, *Cynodon dactylon* and the Tambookie grasses, *A. nardus* var. *validus*, *A. auctus*, *A. rufus*, *A. dichroos*, *A. cymbarius* var. *lepidus*; but many of these, as already indicated, are important in other seres as well.

6. TREE VELD.

(Pl. XXIII, fig. 2; Pl. XXIV, figs. 1 and 2.)

There are various types of tree veld on the coast belt, consisting of more mesophytic species on the south coast and of thorn veld dominated by species of *Acacia* and *Euphorbia* on the drier, hotter portions of the north coast, from Verulam to the Tugela and beyond it in Zululand. The tree veld plant succession for typical thorn veld has been analysed in considerable detail in one of my former papers.¹ Various pioneer species of trees, e. g. the *Acacias*, *Cussonias*, *Euphorbias*, *Celastrus buxifolius*, *Albizzia fastigiata*, *Dichrostachys nutans*, the seeds of which are able to germinate among the grasses of the grassveld and the seedlings of which can withstand full exposure from the start, grow up as isolated specimens, forming a park-like type of plant community. The pioneers are not shrubs as in other forest seres. Many other species both of trees and shrubs (including numerous climbers) which are not able to act as pioneers find a suitable germinating ground under the shade of the pioneer tree, where the soil is loosened and prepared for them by the activities of earthworms, termites, etc. The pioneer itself frequently grows up from an old termite nest, which thus forms the starting-point for the formation of a characteristic clump. The seeds of the majority of the species are distributed by birds, which naturally alight on the branches of the pioneer tree. Fruit-eating bats, too, are very common agents of dispersal. The seeds of some of the pioneers, however, e. g. the *Acacias*, are often distributed uniformly through the grassveld by grazing herbivores.

The pioneers are not only light-demanding xerophytic species, but they are also resistant to grass-fires. The second stage of the succession is seen when the later arrivals grow up round the pioneer tree and tend to smother it. Thus

¹ Bews, J. W., "The Plant Succession in the Thorn Veld," 'South African Journ. of Science,' November, 1917.

characteristic isolated clumps are formed which grow larger. More pioneers fill in the intervening spaces and finally scrub is formed. In the moister climatic areas such scrub may give way later to forest, but in the drier parts the Acacias and Euphorbias remain dominant and the thorn scrub thus formed is a climax type.

The tree veld type of plant succession also occurs in the hydrosere, the pioneers being hygrophilous species of trees which will again be referred to in connection with coast-scrub and forest. The *umDoni* or Waterboom (*Eugenia cordata*) is the most important (Pl. XXIV, fig. 2). It is very common on the south coast behind the dunes, colonising all the moister types of grassveld. It is often followed by *Strelitzia augusta*. The figs (*Ficus capensis* and *F. natalensis*) also belong to the hydrosere and act as pioneers. Other species will be referred to later.

Tree veld generally is most abundant in the neighbourhood of scrub of one kind or another, either xerophytic, thorny and succulent scrub in the drier parts or mesophytic scrub in moister parts, or hygrophilous scrub in very moist situations. The scrub species are naturally transported into the tree veld, but the essential point on which emphasis is laid is that the tree species are the pioneers and only a few are able to act as such, and a park-like type is the precursor of the denser scrub.

Since the total list of species which occur in coast tree veld is somewhat extensive, it has been thought well to arrange them according to the families to which they belong, indicating at the same time the nature of their growth forms and giving their relative frequency. The symbols used have the usual significance (d. = dominant, l.d. = locally dominant, a. = abundant, l.a. = locally abundant, f. = frequent, l. = local, o. = occasional, r. = rare).

CAPPARIDÆ.—*Cadaba natalensis* (261), scrambler (o.); *Niebuhrria triphylla*, shrub or tree (o.); *Capparis citrifolia* (l.a.), *C. corymbifera* (379) (l.f.), *C. gueinzii* (l.a.), *C. zeyheri* (214) (l.a.), all climbers. These climbing species naturally appear after the pioneers have become established.

They illustrate the tropical nature of the coast belt vegetation and show the connection between tree veld and other coast scrub.

BIXINEÆ.—*Scolopia zeyheri*, tree or shrub (f.), *Aberia caffra*, shrub or small tree (f.); *Trimeria grandifolia* (in moist places), tree (f.).

PITTOSPOREÆ.—*Pittosporum viridiflorum* (in moist places), tree (f.).

STERCULIACEÆ.—*Dombeya rotundifolia* (o.), *D. natalensis* (o.), shrubs or small trees.

TILIACEÆ.—*Grewia caffra* (42), shrub or tree (a.); *G. lasiocarpa*, shrub (l.f.); *G. occidentalis* (210), shrub (f.). These are often early arrivals after the pioneer tree.

RUTACEÆ.—*Toddalia lanceolata*, tree (l.f.); *Clausena inæqualis* (66), tree (f.); *Xanthoxylon capense*, tree (o.). On the whole, these are more characteristic of true forest.

OCHNACEÆ.—*Ochna arborea*, small tree (l.f.); *O. atropurpurea*, shrub (l.f.).

BURSERACEÆ.—*Commiphora harveyi*, tree (f.); *C. caryæfolia*, tree (f.).

MELIACEÆ.—*Ekebergia capensis*, tree (l.f.).

CELASTRINEÆ.—*Celastrus buxifolius* (535), tree (a.), pioneer; *C. cordatus*, shrub (o.); *C. undatus*, tree (f.); *Elæodendron capense*, small tree (f.); *E. croceum*, tree (f.); *E. sphærophyllum*, small tree (f.); *E. velutinum*, tree (o.); *Putterlickia verrucosa*, shrub (f.).

RHAMNEÆ.—*Zizyphus mucronata* (47), tree (l.a.); *Scutia commersoni*, shrub, tree or climber (l.d.); *Helinus ovata*, scrambler (f.).

AMPELIDEÆ.—*Vitis cuneifolia* and many other species of vine are abundant and characteristic, often half-smothering the pioneer species. (See under "Scrub" for the coast veld species.)

SAPINDACEÆ.—*Ptæroxylon utile*, tree (o.); *Schmiedelia monophylla*, tree (o.); *S. erosa*, shrub (l.f.); *Hippobromus alatus*, shrub (f.); *Bersama lucens* (88),

small tree confined to coast belt (o.); *Dodonæa viscosa*, shrub (l.).

ANACARDIACEÆ.—*Rhus*, many species (a.) (see under "Coast-scrub"); *Harpephyllum caffrum*, tree (l.f.); *Sclerocarya caffra* (307), tree (l.a.).

LEGUMINOSÆ.—*Milletia caffra*, tree (l.a.); *Dalbergia obovata* and *D. armata*, woody lianes (l.a.); *Erythrina caffra* (542), tree (a.); *E. tomentosa*, tree (a.); *Schotia brachypetala* (390), tree or shrub (f.); *Albizzia fastigiata* (27), tree (l.a.); *Dichrostachys nutans*, small tree (l.d.); *Acacia arabica* var. *kraussiana*, tree (d.); *A. horrida*, tree (l.); *A. caffra*, tree (l.d.); *A. gerrardi*, tree (l.); *A. hirtella*, tree (?); *A. natalitia*, tree (?); *A. pennata* (244), climber (f.); *A. kraussiana* (245), climber (f.); *Entada natalensis* (34), climber (l.a.), with many other shrubs. (See under "Coast-scrub.")

This family is by far the most important in the thorn veld, the Acacias or thorns being the dominant trees. *Dichrostachys nutans* is a characteristic coast belt species not found in the midlands, similar in habit to the Acacias, i. e. of the umbrella-form. *Albizzia fastigiata*, the Flatcrown, occurs also in scrub and forest.

RHIZOPHOREÆ.—*Cassipourea verticillata*, tree (l.).

COMBRETACEÆ.—*Combretum kraussii* (f.), *C. gueinzii* (o.), *C. erythrophyllum* (o.), all small trees; *C. bracteosum* (77), shrub or creeper (o.).

LYTHRARIÆ.—*Heteropyxis natalensis*, shrub (r.)

SAMYDACEÆ.—*Homalium rufescens*, shrub (l.)

ARALIACEÆ.—*Cussonia umbellifera* (l.d.), *C. spicata* (a.), *C. natalensis* (o.), all trees.

RUBIACEÆ.—*Randia dumetorum* (392) (a.); *R. rudis* (o.); *Gardenia globosa* (376) (o.); *Vangueria infausta* (a.); *V. lasiantha* (a.); *V. latifolia* (a.); *P. obovata* (o.); *P. gueinzii*, creeper (f.); *Pavetta caffra* (f.); *P. lanceolata* (f.), shrubs or small trees occurring also in coast scrub.

COMPOSITEÆ.—*Tarchonanthus camphoratus*, tree (o.);

Brachylæna discolor, tree (f.); *B. elliptica*, tree (o.); *Osteospermum moniliferum*, shrub (f.), with numerous other undershrubs. (See under "Coast Scrub.")

PLUMBAGINEÆ.—*Plumbago capensis*, climber (l.a.).

MYRSINEÆ.—*Myrsine melanophleos*, tree (f.); *Mæsa lanceolata*, shrub or small tree (f.), usually in rocky places.

SAPOTACEÆ.—*Sideroxylon inerme*, tree (a.); *Mimusops obovata*, tree (o.).

EBENACEÆ.—*Royena cordata* (o.); *R. pallens* (f.), near water; *R. villosa* (20) (o.), shrubs or small trees; *Euclea lanceolata*, shrub or tree (f.).

OLEACEÆ.—*Jasminum multipartitum* (328) (a.) and *J. streptopus* (50) (o.), climbing shrubs; *Olea verrucosa*, tree (l.a.), in rocky places; *Schrebera saundersiæ* (536), shrub or small tree.

APOCYNACEÆ.—*Carissa arduina* (203), shrub (f.); *Rauwolfia natalensis*, tree (o.), near water, but more characteristic of the forest sere. *Acocanthera venenata*, shrub or tree (l.a.); *Voacanga dregei* (f.), near water, but more often in the forest sere.

ASCLEPIADACEÆ.—Many climbing species (a.). (See under "Coast Scrub.")

LOGANIACEÆ.—*Nuxia congesta*, small tree (f.); *Buddleia salviæfolia*, shrub (f.); *Strychnos spinosa*, small tree (f.); *Chilanthus oleaceus*, straggling shrub (a.); *C. dyssophyllus*, straggling shrub (l.f.)

BORAGINEÆ.—*Ehretia hottentottica*, small tree (a.); *Cordia caffra* (508), shrub or small tree (a.).

PROTEACEÆ.—*Faurea saligna*, tree (l.d.), on sandstone only.

THYMELIACEÆ.—*Peddiea africana* (87), small tree or shrub (a.).

LORANTHACEÆ.—Species of *Loranthus* and *Viscum* (f.). (See under "Coast Scrub.")

SANTALACEÆ.—*Osyridocarpus natalensis*, straggler (o.); *Osyris abyssinica*, shrub (o.).

EUPHORBIACEÆ.—*Euphorbia tirucalli*, tree (l.d.); *E. ingens*, tree (l.d.); *E. cooperi*, small tree (l.); *E. similis*, tree (?); *E. evansii*, tree (l.); *E. triangularis*, tree (o.); *E. grandidens*, tree (r.) or doubtful for Natal; *E. epicyparissias*, shrub (f.); *E. kraussiana* (l.); *Drypetes* sp. (*Cyclostemon argutus*, tree (o.)); *Bridelia micrantha*, tree (l.); *Spirostachys africana*, tree (l.a.); *Dalechampia capensis* (515), climber (a.).

Next to the Leguminosæ this is the most important family. The tree-Euphorbias are dominant over hot, dry, rocky or sandy slopes, forming succulent scrub, a very definite climax type. Elsewhere they are subdominant to the Acacias. *E. ingens* is a very large obconical species often 30 ft. or more in height, the most conspicuous in thorny scrub even when not the most abundant.

URTICACEÆ.—*Ficus capensis* (a.); *F. natalensis* (a.); *F. nekbudu* (o.); *F. sycomorus* (o.); *Celtis kraussiana* (28), (o.); *Trema bracteolata* (356), (o.). All trees usually in moist places along streams and belonging rather to the forest sere, but occurring as isolated pioneers sometimes.

SCITAMINEÆ.—*Strelitzia augusta* (l.d.), very abundant all along the coast behind the dunes as well as in the psammophilous bush.

PALME.—*Phœnix reclinata*, tree (l.a.), forming small clumps or growing quite isolated. *Hyphæne crinita*, small bush or tree (l.d.)—an important pioneer.

LILIACEÆ.—*Asparagus* spp. (a.). (See under "Coast Scrub.") *Aloe cooperi* (o.), *A. kraussii* (o.), *A. saponaria* (f.), *A. bainesii* (o.), *A. boylei* (o.), *A. parviflora* (o.), on dry rocky slopes.

CYCADACEÆ.—*Encephalartos ghellinckii* (o.), *E. altensteinii* (o.), *E. villosus* (f.), with one or two other species (o.) and *Stangeria paradoxa* (o.).

A careful comparison of the above list with that given later for coast scrub will show that while the majority of the species are common to both yet the dominant species

may be only occasional in the scrub. The thorny scrub, which is the climax of the thorn veld, is much more xerophytic than the scrub which is a stage in the forest succession, especially in its dominant species, the *Acacias*, *Euphorbias*, etc. Nevertheless, many of the more mesophytic scrub species are brought even into thorn veld, the seeds, as explained, being carried by birds. If these more mesophytic species manage to oust the pioneer thorn trees completely, then the thorn scrub also becomes transitional to forest, but it is only in the more favourable localities that this can happen.

While several of the dominant species have a wider range throughout the hot dry river valleys of the midlands and are able to withstand severe frosts in winter, the following are confined to the coast belt, or at any rate to frost-free localities. They are mostly tropical in their affinities: *Erythroxylon monogynum*, *Dodonaea viscosa*, *Bersama lucens* (88), *Sclerocarya caffra* (307), *Milletia caffra* (32), *Albizzia fastigiata* (27), *Dichrostachys nutans* (243), *Cassipourea verticillata*, *Heteropyxis natalensis*, *Homalium rufescens*, *Cussonia umbellifera*, *Tricalysia lanceolata* (231), *Strychnos spinosa*, *Cordia caffra* (508), *Cyclostemon argutus*, *Bridelia micrantha*, *Spirostachys africana* and the palms, *Phoenix reclinata* and *Hyphæne crinita*. This list is sufficiently representative to mark off fairly sharply the coast belt tree veld from that of the midlands.

The following are the most important types of tree veld on the coast belt:

(a) **ILALA-PALM VELD.**—This important type is very common on the drift sands behind the shore-line of sand-dunes. It is dominated by *Hyphæne crinita* (Pl. XXIV, fig. 2), the Ilala palm, which is used by the natives for making baskets. While it occurs all along the coast, it is particularly well-developed around Port Shepstone, and again in Zululand. *Hyphæne* acts as a pioneer, and being an intense light-demander it is easily killed out by taller-growing species.

It often forms small clumps by itself, or it is associated with such species as *Antidesma venosum*, *Strychnos spinosa*, *Brachylaena discolor*, *Clerodendron glabrum*, *Erythrina caffra*.

(b) *VANGUERIA INFAUSTA*.—It is rather common as a pioneer all along the south coast. It is a low-growing species, either a shrub or small tree, as a rule.

(c) *ROYENA* SP. (*VILLOSA* ?).—This shrub is very commonly associated with the *Vangueria*.

The above are very primitive types in the succession, and several other species might be included with them.

(d) *MESOPHYTIC TREE VELD*.—Where the majority of the species listed above occurs, the mesophytic tree veld leads on to mesophytic scrub, which will be dealt with in the following section. Such tree veld is common everywhere along the south coast from Port Shepstone to Durban and along the north coast to Zululand, in all the moister situations, e. g. in the sheltered valleys and where the rainfall is slightly higher. On the north coast, however, it is mixed with the more xerophytic thorn veld, dominated by *Acacias*.

(e) *HYGROPHILOUS TREE VELD*.—This type occurs in situations near the stream banks or in soil where abundant water occurs at no great depth, and is common all along the coast, especially behind the dunes. The *umDoni*, *Eugenia cordata*, is the most characteristic tree (Pl. XXIV, fig. 2), but *Ficus capensis*, *F. natalensis*, *Rauwolfia natalensis*, *Acacia caffra*, *Combretum salicifolium*, *Trema bracteolata*, *Pittosporum viridiflorum*, *Rhus viminalis*, *Royena pallens*, *Macaranga capensis*, *Grewia lasiocarpa*, *Melianthus* spp., *Cliffortia strobilifera*, *Trimeria grandifolia*, *Burchellia capensis*, *Voa-canga dregei*, *Psoralea pinnata*, *Gnidia ovalifolia*, *Ochna atropurpurea*, *Spirostachys africana*, *Myrica conifera*, in so far as they occur in tree veld, all belong to the same class. The succession advances quickly towards scrub or forest.

(f) *ROCKY TREE VELD*.—This is another primitive type, like

all the above. Certain species are peculiarly characteristic of rocky situations, but these are not so frequent on the coast belt as in the midlands. The species are *Encephalartos altensteinii*, *E. ghellinckii*, *E. villosus*, *Olea verrucosa*, *Mæsa lanceolata*, *Plectronia ciliata*, *Carissa arduina*, and the *Euphorbias* detailed in the general list given above. The type again gives way to close scrub and forest.

(g) THORN VELD.—This type advances towards a thorny scrub, which appears to be the climax for the drier areas on the north coast around Verulam and again north of Stanger towards the Tugela and in Zululand. The factors which determine it have already been outlined, viz. the greater range of temperatures, the slightly lessened rainfall, the full exposure to dry, hot "foehn" winds, and the nature of the soil with a hard shale usually near the surface. The dominant species are the *Acacias*, *Dichrostachys nutans*, and the *Euphorbias* (see general list above), but as the succession advances many of the less hygrophilous species also come in though they do not manage to assume dominance. The type as it occurs near Verulam is illustrated in Pl. XXIV, fig. 1.

7. COAST SCRUB.

(The initial stages of the forest sere, Pl. XXIV, fig. 2.)

This unstable transitional type is more mesophytic than the thorn scrub. It is widely developed, and formerly was very extensive, but at the present time, since so much of it has been cleared to make way for sugar-cane, it is patchy. It follows in the hydrosere after vlei grasses, and in the xerosere after Tambookie associates, or it is formed from mesophytic tree veld as described above. On steep, rocky banks or in dongas and ravines it often develops at a much earlier stage of the succession, following immediately on lithophilous vegetation. Even the taller trees may sometimes be the earliest arrivals, their seedlings finding the necessary shade and

shelter in deep rock-crevices and among boulders. Scrub is always found as a marginal belt to forest, to which it gradually gives way as the taller trees kill out the light-demanding shrubs and small trees by shading them. While the scrub, as a whole, represents a transitional stage, and as such is of a very mixed character, there can be recognised two or three stages in its own development.

(a) TAMBOOKIE ASSOCIES.—This type is transitional between grassveld and scrub, between vlei grasses and scrub, and it develops in rocky places, in dongas, and sometimes in disturbed soil or cultivated land. It is marginal to scrub in the same way as scrub is to forest. The name Tambookie is applied to any of the tall-growing species of *Andropogon*, e. g. *A. nardus* var. *validus*, *A. auctus*, *A. dregeanus*, *A. rufus*, *A. dichroos*, *A. cymbarius* var. *lepidus*, all very similar in their growth-forms and all occurring on the coast belt. They grow to a height of six to eight feet or more, forming rather compact tufts. Another very characteristic grass constantly occurring in this zone on the coast belt is *Setaria sulcata*, which has very broad, sulcate leaves. *Setaria lindenbergiana* is somewhat like it, but not so common. *Erianthus capensis*, *Arundinella eckloni*, *Panicum crus-pavonis* and many of the group of vlei grasses already described are associated. The moist grass zone around the scrub is also the favourite habitat for a great many other grasses, especially the coast *Panicums*, which are also frequently ruderal (*Panicum brizanthum*, *P. filiculme*, *P. hymenochilum*, *P. æquinerve*, *P. perlaxum*, *P. chusqueoides*, *P. laticomum*, *P. zizanioides*, *P. deustum*, *P. maximum*, *P. lævifolium*, *P. proliferum*, *P. curvatum*). They are widely scattered but not abundant in any one spot. Certain species of *Eragrostis* are also characteristic, e. g. *E. ciliaris*, *E. lap-pula*, *E. gangetica*.

(b) ZONE OF LOW SHRUBS AND HERBS.—Here there are numerous herbaceous creepers or climbers. This is probably the most mixed type of all, containing the largest number of

species on the coast belt. It is not very sharply marked off from the next zone, for seedlings of the trees may usually be found among it. The Acanthaceæ, Leguminosæ, Compositæ, Cucurbitaceæ, Convolvulaceæ, Polygalaceæ, Malvaceæ, Labiatæ, Orchidaceæ, Iridaceæ, Amaryllidaceæ, Liliaceæ, Commelinaceæ are all abundantly represented, but it has been thought better not to give separate lists of species for this stage, but to include them all in the list given below, the growth-form which is given in each case being a sufficient guide as to the place of each species in the succession.

(c) ZONE OF TALL SHRUBS AND TREES.—A large number of species are also included here. Tall, woody lianes are common, the whole forming a tangled, impenetrable mass. There are a number of epiphytes and parasites. True forest trees also occur, many of them being somewhat variable in their growth-forms, and only in the more favourable situations forming high forest. Over seven hundred species can be referred to coast belt scrub, and the long list is arranged, as in the case of the tree veld, with symbols of frequency used as before and notes on the growth-forms, etc.

RANUNCULACEÆ.—*Clematis grata* (o.), *C. owenii* (o.), climbers; *Knowltonia brevistylis* (o.), herb, moist shady places around margin.

ANONACEÆ.—*Uvaria caffra* (241), climber (f.); *Artabotrys monteiroæ*, climber (r.); *Popowia caffra*, straggling woody creeper (f.); *Anona senegalensis*, shrub or small tree (l.a.)—a tropical family.

MENISPERMACEÆ.—*Cissampelos pariera* (f.), *C. torulosa* (f.), both climbing species occurring also in the tropics.

CAPPARIDEÆ.—*Neibuhria rosmarinoides* (315), undershrub (o.); *N. triphylla*, shrub or tree (f.); *N. woodii*, undershrub (o.); *Cadaba natalensis* (261), scrambler (l.f.); *Mærua angolensis*, shrub (o.); *M. nervosa* (260), shrub (f.); *Capparis citrifolia* (f.); *C. corymbifera* (379), (f.); *C. gueinzii* (f.); *C. zeyheri* (214), (f.), all climbers. Another tropical family. The frequency of all the above-

mentioned species illustrates the tropical nature of the coast belt scrub.

VIOLACEÆ.—*Alsodeia* (*Rinorea*) *ardiseæfolia*, small tree (a.).

BIXINÆ.—*Oncoba kraussiana* (172), small tree (f.); *O. spinosa*, spiny shrub (o.); *O. tettensis*, shrub (o.); *Rawsonia lucida* (575), shrub or small tree (f.); *Scolopia zeyheri*, tree or shrub (a.); *S. eckloni*, tree or shrub (f.), *S. gerrardi*, tree or shrub (o.); *Dovyalis zizyphoides*, shrub or small tree (f.); *D. celastroides*, shrub or small tree (f.); *Aberia caffra*, shrub or small tree (o.); *Trimeria grandifolia*, tree (a.).

PITTOSPOREÆ.—*Pittosporum viridiflorum*, tree (a.).

POLYGALÆ.—*Polygala myrtifolia* (f.), *P. capillaris* (o.), *P. confusa* (o.), *P. durbanensis* (r.), *P. oppositifolia* (f.), *P. serpentaria* (o.), *P. rarifolia* (f.), *P. virgata* (f.), light-demanding small shrubs near the outer margin.

GUTTIFERÆ.—*Garcinia gerrardi*, small tree (l.a.).

MALVACEÆ.—*Pavonia dregei* (o.), *P. kraussiana* (o.), *P. columella* (o.), *P. odorata* (o.), *Hibiscus calycinus* (f.), *H. pedunculatus* (533), (f.); *H. natalitius* (o.), *H. furcatus* (o.), *H. pusillus* (o.), *H. æthiopicus* (o.), *H. gossypinus* (f.), *Sida rhombifolia* (a.), *S. spinosa* (o.), *S. acuta* (f.), *S. cordifolia* (f.), *S. triloba* (o.). Fibrous shrubs common near the outer margin.

STERCULIACEÆ.—*Cola natalensis*, small tree (r.); *Dombeya rotundifolia* (l.f.), *D. natalensis* (f.), shrubs or small trees.

TILIACEÆ.—*Grewia caffra* (42), shrub or tree (a.); *G. lasiocarpa*, rambling shrub (f.); *G. occidentalis* (210), shrub or tree (a.); *Triumfetta effusa* (318), (a.); *T. rhomboidea* (262), (a.), both shrublets.

LINEÆ.—*Erythroxylon emarginatum* (r.), *E. pictum* (r.), *E. monogynum* (r.), all small trees rare on coast-belt.

MALPIGHIACEÆ.—*Acridocarpus natalitius* (f.), *Sphedamnocarpus pruriens* (400), (o.), both climbers.

GERANIACEÆ.—*Geranium ornithopodum* (o.), *Pelargonium australe* (o.), *P. pulverulentum* (o.), *Impatiens capensis* (a.), herbs in moist shady places around the margins or as undergrowth.

RUTACEÆ.—*Barosma lanceolata*, shrub (o.), near outer margin; *Calodendron capense* (562), tree (a.); *Toddalia lanceolata*, tree (a.); *T. natalensis*, small tree (f.); *Clausena inæqualis* (66), tree (a.); *Xanthoxylon capense*, tree (o.); *X. thunbergii*, tree (o.).

All the Rutaceous trees are characteristic also of true forest.

OCHNACEÆ.—*Ochna arborea*, small tree (a.); *O. atropurpurea*, shrub (f.).

BURSERACEÆ.—*Commiphora caryæfolia* (a.), *C. harveyi* (a.), both trees.

MELIACEÆ.—*Turræa floribunda* (246), (r.); *T. obtusifolia* (l.f.), tropical shrubs; *Ekebergia capensis*, tree (a.); *E. meyeri* (6), tree (a.); *Trichilia emetica* (80), large tree (f.); *T. alata* (209), small tree (r.); *T. dregei*, small tree (f.).

OLACINÆÆ.—*Apodytes dimidiata* (18), tree (a.); *Pyrenacantha scandens*, climber (o.).

CELASTRINÆÆ.—*Celastrus* (*Gymnosporia*) *acuminatus* (267), tree (o.); *C. buxifolius* (535), tree (a.); *C. cordatus*, shrub (f.); *C. procumbens*, shrub (o.); *C. undatus*, tree (a.); *Pterocelastrus variabilis*, tree (o.); *Putterlickia verrucosa*, shrub (l.a.); *Elæodendron capense*, small tree (a.); *E. croceum*, tree (o.); *E. velutinum*, tree (a.); *E. sphærophyllum*, small tree (f.); *Salacia alternifolia* (372), shrub (o.). This is one of the most important families of trees and shrubs in coast scrub.

RHAMNÆÆ.—*Zizyphus mucronata* (a.-l.d.), the Wait-a-bit thorn-tree; *Scutia commersoni*, shrub, tree or climber (a.); *Noltea africana*, shrub (r.); *Helinus ovata*, scrambler (a.); *Rhamnus zeyheri* (590), small tree (l.).

AMPELIDÆÆ.—*Vitis* (*Cissus*) *cuneifolia*, shrub or climber (a.); *V. capensis* (a.), *V. cirrhosa* (a.), *V. fragilis* (o.), *V. gracilis* (o.), *V. hypoleuca* (286), (a.); *V. natalitia*

(f.), *V. orientalis* (o.), *V. quadrangularis* (o.), *V. rhomboidea* (f.), *V. thunbergii* (o.), *V. tetragona* (o.), *V. lanigera* (o.), *V. semiglabra* (o.). All climbers ("monkey-ropes"). These wild vines are a very common feature of all coast scrub and are particularly abundant in the marginal zone.

SAPINDACEÆ.—*Cardiospermum halicacabum*, herb (f.) around margin; *Schmidelia decipiens*, shrub (f.); *S. erosa*, shrub (a.); *S. africana* (572), shrub (f.); *S. monophylla*, tree (o.); *S. rehmanniana*, shrub (o.); *Hippobromus alatus*, shrub (f.); *Sapindus oblongifolius* (89), small tree or shrub (o.); *Dodonæa viscosa*, shrub (l.); *Ptæroxylon utile*, tree (l.); *Bersama lucens* (88), small tree (f.). Another important family of trees and shrubs in coast scrub.

ANACARDIACEÆ.—*Protorhus longifolia* (69 and 383), large tree dominant as the scrub develops into true forest; *Rhus lævigata*, also a large tree (f.); *R. lucida*, *R. dentata*, *R. natalensis*, *R. obovata*, *R. parvifolia*, *R. pyroides*, *R. tridentata*, *R. villosa*, small trees or shrubs very common around the margin; *Harpephyllum caffrum*, tree (f.); *Sclerocarya caffra* (307), tree (l.d.); *Smodingium argutum*, shrub or small tree (l.a.). A still more important family, including dominant or locally dominant species.

CONNARACEÆ.—*Cnestis natalensis*, woody liane (f.).

LEGUMINOSÆ.—This large family includes a number of important trees: *Albizzia fastigiata* (27), (a. or l.d.); *Milletia caffra* (32), (l.a.); *Schotia brachypetala* (390), (o.); *Erythrina caffra* (542), (a.); *Baphia racemosa* (19), (f.); *Calpurnia lasiogyne* (4), tree or shrub (o.). The woody lianes, *Dalbergia obovata* (a.) and *D. armata* (79), (a.) climb over the trees throughout the scrub.

The other species are more marginal and include a large number of herbs, shrubs and stragglers or climbers, e.g. *Lotononis cytisoides*, *Aspalathus spinosa*, *Lebeckia mucronata*, *Crotalaria capensis* (92), *Argyrolobium andrewsianum*, *A. ascendens*, *A. reflexum*, *A. san-*

dersoni (228), *Psoralea caffra*, *P. pinnata*, *Indigofera arrecta*, *I. cylindrica*, *I. dregeana*, *I. endecaphylla*, *I. micrantha*, *I. polycarpa*, *I. tetragonoloba*, *I. velutina*, *I. vestita*, *Tephrosia discolor*, *T. kraussiana* (249), *T. polystachya*, *Sesbania aculeata*, *S. ægyptiaca*, *Lessertia perennans*, *L. tenuifolia*, *Smithia sensitiva*, *Desmodium dregeanum*, *D. gangeticum*, *D. incanum*, *D. paleaceum*, *D. scalpe*, *Glycine javanica*, *Teramnus labialis*, *Canavalia obtusifolia*, *C. bonariensis*, *C. ensiformis*, *Dolichos biflorus*, *D. lablab*, *Rhynchosia minima*, *R. sigmoides*, *Bauhinia tomentosa* (399), *Calpurnia villosa*, *C. sylvatica*, *Cassia comosa*, *C. mimosoides*, *C. obovata*, *C. occidentalis*, *C. tomentosa*, *Entada natalensis* (34), *Acacia kraussiana* (245), *A. pennata* (244).

The only *Acacias* are the two climbers last mentioned. The tree *Acacias*, which are dominant in thorn scrub, rarely occur in the more mesophytic coast scrub; though several of the species named above do occur in the thorn scrub after the pioneer thorn trees have prepared the way for them and the Flatcrown, *Albizzia fastigiata*, is common in both types.

ROSACEÆ.—*Pygeum africanum*, tree (o.); *Rubus pin-natus*, scrambler (a.).

CRASSULACEÆ.—*Kalanchoe rotundifolia* (94), herb (f.) in light shade around the margin.

RHIZOPHOREÆ.—*Cassipourea verticillata*, tree (o.).

COMBRETACEÆ.—*Combretum kraussii* (o.), *C. gueinzii* (o.); *C. erythrophyllum* (o.), all small trees commoner in the midlands. *C. bracteosum* (77), creeper (f.).

MYRTACEÆ.—*Eugenia cordata*, tree (a. or l.d.), always near water, a pioneer in the hydrosere and belonging rather to forest; *E. capensis*, shrublet (l.d.) facing the sea.

MELASTOMACEÆ.—*Dissotis eximia* (f.), *D. incana* (o.); *D. phæotricha* (o.), herbs in moist places around the margin.

LYTHRARIÆ.—*Heteropyxis natalensis*, shrub (o.); *Rhynchocalyx rawsonioides*, shrub (r.).

PASSIFLORACEÆ.—*Ophiocaulon gummifera* (11), climber (f.).

SAMYDACEÆ.—*Gerrardiana foliosa*, shrub (l.a.); *Homalium rufescens* (529), much branched shrub (o.).

CUCURBITACEÆ.—*Cephalandra palmata* (283), *Trochomeria sagittata*, *T. pectinata*, *T. garcini* (570), *Peponia mackenii*, *Sphærosicyos sphæricus* (289), *Momordica charantia*, *M. balsaminea*, *M. involucrata* (516), *Cucumis fagarei*, *C. hirsutus*, *C. metuliferus*, *Citrullus vulgaris*, *Coccinea palmata*, *Kedrostis foetidissima*, *K. glauca* (574), *Melothria parvifolia*, *M. punctata*, *Toxanthera natalensis*, *Gerrardanthus macrorrhiza*, *Lagenaria vulgaris*, all climbers or stragglers frequent around the margin.

BEGONIACEÆ.—*Begonia dregei* (f.), *B. suffruticosa* var. *gueinziana* (f.). Herbs in moist shady places.

AIZOACEÆ.—*Mesembrianthemum edule* (o.), around the margins.

UMBELLIFERÆ.—*Peucedanum capense* (o.), *Selinum suffruticosum* (o.), around the margin.

ARALIACEÆ.—*Cussonia spicata* (f.) (Pl. XXIII, fig. 2), *C. umbellifera* (a.), *C. chartacea* (o.), *C. natalensis* (o.), all trees.

RUBIACEÆ.—*Burchellia capensis* (a.); *Randia dumentorum* (392), (a.); *R. rudis* (o.); *Gardenia globosa* (376), (a.); *G. thunbergii* (40), (f.); *G. citriodora* (25), (o.); *G. gerrardiana* (565), (o.); *Oxyanthus latifolius* (f.); *O. natalensis* (26), (f.); *Tricalysia lanceolata* (231), (f.); *T. floribunda* (f.); *T. sonderiana* (293), (f.); *Plectronia locuples* (o.); *P. ciliata* (f.); *P. spinosa* (321), (a.); *P. gueinzii*, creeper (a.); *P. obovata* (o.); *Vangueria infausta* (a.); *V. lasiantha* (f.); *V. latifolia* (a.); *Pavetta caffra* (o.); *P. lanceolata* (a.); *P. obovata* (313), (f.); *Psychotria capensis* (329), (a.) (often in dense shade). All shrubs or small trees very common and characteristic of coast scrub, especially near the margin. The *Vangueria*s spread through the grassveld and are often

important pioneers in the establishing of scrub. Several of the species also are frequent in thorn veld, c f. list given above. *Galopina oxyspermum* (f.), *Anthospermum lanceolatum* (f.), *Mitracarpum dregeanum* (o.), *Rubia cordifolia* (f.), climber, are herbaceous and occur near the outer edge in moist places.

DIPSACEÆ.—*Cephalaria attenuata*, herb (o.), around outer margin.

COMPOSITÆ.—The only trees in the scrub proper belonging to this large family are *Brachylaena elliptica* (a.), *B. discolor* (23 and 24), (a), and *Tarchonanthus camphoratus* (a.).

There are a few common climbers: *Senecio tamoides* (95), (a.); *S. macroglossus* (523), (a.); *S. deltoideus* (382), (a.); *Vernonia angulifolia* (543), (f.); *V. anisochætoides* (268), (f.), and *Mikania scandens* (f.).

The others are shrubby or half herbaceous: *Vernonia mespilifolia* (f.); *V. woodii* (f.); *Aster quinquenervis* (f.); *Nidorella auriculata* (a.); *Helichrysum cymosum* (o.); *H. decorum* (o.); *H. fulgidum* (a.); *H. teretifolium* (327), (a.); *Cassinia phylicifolia* (a.); *Stœbecinerea* (f.); *Athrixia phylicoides* (o.); *Pulicaria capensis* (f.); *Wedelia natalensis* (a.); *Athanasia acerosa* (l.d.); *Schistostephium cratægifolium* (f.); *S. rotundifolium*; *S. sp.* (*Tanacetum griseum*) (o.); *S. sp.* (*Tanacetum heptalobum*) (o.); *S. sp.* (*Tanacetum hippæfolium*) (o.); *Senecio paniculatus* (502), (f.); *S. lanceus* (f.); *S. hastulatus* (f.); *S. decurrens* (f.); *Osteospermum moniliferum* (55), (a.); *O. helichrysoides* (o.); *Berkheya maritima* (l.); *B. subulata* (f.); *Artemesia afra* (l.d.).

Several of the above are very important pioneers, especially *Artemesia afra*, *Athanasia acerosa*, and the *Vernonias*. These form distinct consocieties in the marginal transitional zone, but they are soon killed out by shading. The family, as a whole, is characteristic of the extreme outer margin, the species being light-demanders and relatively xerophytic, c f. the *Acanthaceæ* with which they seldom mix to any extent.

CAMPANULACEÆ.—*Lobelia coronopifolia* (o.), *L. radi-*

cans (o.), *Roella glomerata* (o.), herbs around the outer margin.

PLUMBAGINÆ.—*Plumbago capensis*, climber (o.).

PRIMULACÆ.—*Samolus valerandi*, cosmopolitan herb (l.a.), around edge.

MYRSINÆ.—*Mæsa lanceolata* (*M. rufescens*), shrub or tree (a.), often a pioneer in rocky places; *Myrsine melanophleas* (259), large tree (a.), moist places; *Embelia kraussii*, shrub or creeper (a.).

SAPOTACÆ.—*Chrysophyllum viridifolium* (569), small tree (r.); *C. natalense* (378), tree (f.); *Sideroxylon inerme*, tree (o.); both characteristic rather of true forest. *Mimusops caffra* (43), tree (o.), but dominant in sand-dune bush; *M. discolor*, tree (o.); *M. concolor*, tree (o.); *M. marginata*, tree (o.); *M. obovata*, tree (o.); *M. oleifolia*, small tree (o.); *M. schinzii*, small tree (o.); *M. woodii*, small tree (o.).

EBENACÆ.—*Royena cordata*, shrub (l.a.); *R. pallens*, shrub (f.); *R. villosa* (201), small tree (f.); *Euclea lanceolata*, shrub or tree (a.); *E. multiflora*, shrub or tree (o.); *E. natalensis* (265), tree (a.); *Maba natalensis*, tree (o.).

OLEACÆ.—*Jasminum multipartitum* (328), climber (a.); *J. streptopus* (50), (a.), climber; *Schrebera saundersiæ* (536), shrub or small tree (r.); *S. obliquifoliolata*, shrub or small tree (r.); *Olea verrucosa*, tree (l.a.), in rocky places; *O. woodiana*, tree (l.f.).

APOCYNACÆ.—*Carissa arduina* (203), shrub (f.); *C. grandiflora*, shrub (l.a.); *Acokanthera spectabilis* (74), (o.); *Rauwolfia natalensis*, tree (l.d.), in the hydrosere; *Strophanthus gerrardi*, climber (f.); *Oncinotis inandensis*, tall herbaceous climber (l.a.); *Wrightia natalensis* (347), shrub (l.f.); *Voacanga dregei*, tree (l.d.), in the hydrosere. This family is important because it contains two trees, *Rauwolfia natalensis* and *Voacanga dregei*, which, together with *Eugenia cordata* and the

figs (see later), act as pioneers along waterways and form a definite stage in the succession to forest.

ASCLEPIADACEÆ.—This family contains a large number of climbing species; very characteristic of coast scrub. The herbaceous non-climbers belong rather to open grassveld and are poorly represented on the coast as compared with the midlands. The following are all climbers:

Cryptolepis capensis (o.); *C. oblongifolia* (513), (f.); *Tacazzea kirkii* (o.); *T. natalensis* (o.); *Clorocodon whytei* (a.); *Secamone gerrardi* (388), (a.); *S. alpini* (o.); *S. frutescens* (o.); *Pentarrhinum insipidum* (517), (f.); *Cynanchum natalitium* (301), (a.); *C. capense* (o.); *C. schistoglossum* (o.); *Sarcostemma viminale* (a.); *Pergularia extensa* (?); *Tylophora anomala* (o.); *T. flanagani* (o.); *T. lycioides* (o.); *Marsdenia* (Dregia) *floribunda* (86), (a.); *Telosma africana* (566), (a.); *Gymnema sylvestre* (o.); *Riocreuxia torulosa* (a.); *Ceropegia setifera* (o.); *C. carnosa* (f.); *C. caffrorum* (592), (f.); *C. woodii* (357), (f.).

Ceropegia scabriflora, *Pachycarpus inconstans*, *P. grandiflorus*, *Asclepias brevicuspis*, *A. albens*, *A. præmorsa*, *Schizoglossum robustum*, *Periglossum mackenii*, *Sphærocodon obtusifolium* are herbaceous non-climbers frequent around the outer margin.

LOGANIACEÆ.—*Nuxia congesta*, small tree (f.); *N. floribunda* (59), tree (f.); *N. oppositifolia*, shrub (f.); *Chilianthus dyssophyllus*, straggling shrub (a.); *C. oleaceus*, straggling shrub (o.); *Buddleia salviæfolia*, shrub (a.); often a pioneer forming consocieties around margin, *B. auriculata*, shrub (f.); *Strychnos atherstonei*, tree (l.); *S. gerrardi* (16), tree (f.); *S. spinosa*, small tree (l.f.); *S. henningsii*, tree (f.).

GENTIANACEÆ.—*Chironia krebsii* (o.); *C. peduncularis* (o.); *C. purpurascens* (288), (f.); *Belmontia grandis* (f.), marginal herbs or shrubs.

BORAGINÆÆ.—*Cordia caffra* (508), shrub or small tree (f.); *Ehretia hottentottica*, small tree (a.).

CONVOLVULACEÆ.—*Ipomæa albivenia* (38), *I. cardiosepala*, *I. crassipes*, *I. digitata*, *I. ficifolia* (525), *I. geminiflora*, *I. obscura*, *I. palmata*, *I. purpurea*, (93), *I. tetraptera*, *I. wightii*, *Merremia angustifolia*, *Convolvulus calycinus*, *C. farinosus*, *C. natalensis*, *C. sagittatus*, *Hewittea bicolor* (281), *Jacquemontia capitata* (13), *Evolvulus alsinoides*, *Falkia oblonga*, *Dichondra repens*, *Astrochlena grantii*, all climbers, common or abundant near outer margins, often forming a dense leafy covering over the trees or shrubs, by which they are supported. *Cuscuta cassytoides* and *C. natalensis* are parasites on marginal shrubs.

SOLANACEÆ.—*Solanum auriculatum* (352), shrub (a.); *S. acanthoideum*, herbaceous (f.); *S. duplusinuatum*, herb (o.); *S. geniculatum*, climbing shrub (f.); *S. exasperatum*, shrub (o.); *S. giganteum*, shrub or small tree (f.); *S. aculeastrum*, shrub (o.); *S. aculeatissimum*, small shrub (o.); *Withania somnifera*, small shrub (f.), all marginal species.

SCROPHULARIACEÆ.—*Diascia racemulosa*, herb (r.); *Nemesia cynanchifolia*, herb (o.); *Dermatobotrys saundersiæ*, epiphytic shrub (r.); *Halleria lucida* (545), shrub or tree (a.); *Anastrabe integerrima* (480), shrub (f.); *Phyllopodium bracteatum*, herb (f.); *Harveya coccinea*, root parasitic herb; *H. squamosa*, root parasite; *H. speciosa*, root parasite; marginal species, with the exception of *Halleria*, not very common.

GESNERACEÆ.—*Streptocarpus*, one or two species (f.) on moist shady banks.

BIGNONIACEÆ.—*Tecomaria capensis* (272), rambling shrub (l.f.).

ACANTHACEÆ.—*Thunbergia natalensis*, shrublet (f.), in shady places; *T. venosa*, straggler (o.); *T. neglecta*, rambler (r.); *T. pondoensis* (340), climber (f.); *T. dregeana*, climber (a.); *T. alata* (300), climber (a.); *Ruellia baurii*, undershrub (f.); *R. patula*, undershrub (f.); *R. ovata*, straggling herb (o.); *Chætacanthus glandulosus*,

herb (f.); *Ch. burchellii*, herb (o.); *Phaylopsis parviflora* (255), small shrub (a.); *Ph. longifolia*, shrublet (o.); *Blepharis boerhaaviæfolia*, undershrub (a.); *B. molluginifolia*, undershrub (f.); *B. setosa*, undershrub (o.); *B. pruinosa*, undershrub (o.); *Sclerochiton harveyanus*, undershrub (f.); *Asystasia coromandeliana*, common weed (a.); *A. varia*, herb (o.); *A. schimperii*, annual herb (f.); *Mackaya bella* (585), shrub (f.); *Barleria elegans*, herb (o.); *B. gueinzii*, herb (o.); *B. barbata*, herb (o.); *B. woodii*, herb (o.); *B. ovata*, herb (f.); *B. obtusa*, herb (a.); *B. meyeriana*, herb (f.); *Ruttya ovata* (514), (a.); *Justicia betonicoides*, shrub (o.); *J. trinervia*, herb (o.); *J. flava*, undershrub (a.); *J. pulegioides*, undershrub (a.); *J. kraussii*, herb (o.); *J. rotundifolia*, herb (o.); *J. campylostemon*, undershrub (a. or l.d.); *J. petiolaris* (347), undershrub (f.); *Monechma bracteatum*, herb (a.); *M. fimbriatum*, shrublet (r.); *Adhatoda duvernoia*, shrub (o.); *A. natalensis*, shrub (o.); *A. andromeda*, shrublet (o.); *Rhinacanthus communis*, rambler (a.); *Isoglossa ciliata*, herb (o.); *I. ovata*, undershrub (f.); *I. woodii* (22), undershrub (a. or l.d.); *I. stipitata*, herb (f.); *I. grantii*, herb (o.); *I. hypoestiflora*, shrub (f.); *I. cooperi*, shrub (o.); *I. delicatula*, herb (o.); *Peristrophe hensii*, undershrub (o.); *P. natalensis*, undershrub (o.); *Hypoestes antennifer* (298), undershrub (f.); *H. verticillaris*, undershrub (a.); *Dicliptera heterostegia*, herb (a.); *D. clinopodia*, herb (f.); *D. quintasii*, herb (o.).

This is the most important family of herbs and undershrubs with a few shrubs and climbers. They are abundant in all the moister situations around the margin. Some of them, e.g. *Isoglossa woodii*, form dense thickets or consociates to the exclusion of most other species, others are common inside the scrub, especially near stream banks and in moist, shady, semi-open spaces. The latter is the favourite habitat for the herbaceous species. The great abundance of *Acanthaceæ* is another illustration of the tropical nature of the mesophytic coast scrub.

VERBENACEÆ.—*Lantana salvifolia*, shrub (f.); *L. camara*, scrambling shrub (a.), introduced; *Lippia asperifolia*, shrub (a.); *Bouchea cuneifolia* (571), undershrub (o.); *Priva leptostachya*, herb (o.); *Verbena officinalis*, herb (o.); *Clerodendron glabrum* (45), shrub or small tree (a.); *C. hirsutum*, undershrub (f.); *C. myricoides* (282), shrub (f.).

LABIATÆ.—*Orthosiphon wilmsii* (598), undershrub (o.); *Syncolostemon parviflorus* var. *dissitiflorus*, undershrub (o.); *S. rotundifolius*, undershrub (o.); *S. densiflorus*, undershrub (f.); *Plectranthus calycinus*, herb (f.); *P. floribundus*, herb (o.); *P. saccatus* (85), undershrub (f.); *P. ciliatus*, herb (f.); *P. laxiflorus*, herb (f.); *P. coloratus* (573), herb (f.); *P. purpuratus*, herb (o.); *P. natalensis*, herb (f.); *P. hirtus*, herb (f.); *P. esculentus*, herb (r.); *P. floribundus*, herb (o.); *P. petiolaris*, herb (f.); *P. tomentosus* (316), herb (o.); *Pycnostachys reticulata*, herb (f.); *Æolanthus parvifolius*, herb (o.); *Endostemon obtusifolius*, herb (f.); *Hyptis pectinata*, annual herb (f.); *Iboza riparia* (1 and 2), herb (a.); *Stachys grandifolia*, herb (o.); *S. galpini*, herb (o.); *S. rudatisii*, herb (r.); *S. nigricans*, herb (o.); *S. sessilis*, herb (o.); *Leucas martinicensis*, annual weed (a.); *Leonotis leonurus* (53), shrub (a.).

This is also an important family of herbs and undershrubs characteristic chiefly of the outer marginal zone, but a few occur in fairly dense shade under the trees. Though the aerial branches are commonly herbaceous many of them have a woody rootstock. They often mix with the numerous Acanthaceæ, but some of them can withstand drier conditions and more exposure and tend to die back in winter.

ILLECEBRACEÆ.—*Pollichia campestris*, undershrub (f.).

AMARANTACEÆ.—Most of the ruderal species are common (vide supra); *Pupalia atropurpurea* (544), straggling herb (f.); *Hermbstædtia caffra*, herb (f.); *Celosia trigyna*, herb (f.); *Psilotrichum africanum*, undershrub (o.); *Ærva lanata*, herb (o.).

PHYTOLACCACEÆ.—*Phytolacca dodecandra*, climber (f.) around margins.

PIPERACEÆ.—*Piper capense*, shrub (f.); *Peperomia reflexa* (f.); *P. arabica* (o.); small, often epiphytic herbs.

LAURINEÆ.—*Cryptocarya latifolia*, large tree (o.); *C. woodii*, small tree (l.f.).

THYMELIACEÆ.—*Dais cotinifolia*, shrub (o.); *Arthrosolen phæotrichus*, undershrub (o.); *Passerina filiformis*, shrub (o.); *P. ericoides*, shrub (o.); *Gnidia ovalifolia* (248), undershrub (f.); *Lasiosiphon macropetalus* (262), shrub (o.); *L. dregeanus*, shrub (o.); *L. anthylloides*, shrub (o.); *L. polyanthus*, undershrub (o.); *L. meisnerianus*, shrub (o.), all marginal but not very common; *Peddiea africana* (87), small tree (a.). All are light-demanding species and rather xerophytic.

LORANTHACEÆ.—*Loranthus dregei* (312), (f.); *L. natalitius* (374), (o.); *L. subcylindricus* (o.); *L. quinque-nervis* (295), (o.); *L. kraussianus* (76), (o.); *L. woodii* (r.); *Viscum obovatum* (o.); *V. pulchellum* (r.); *V. nervosum* (f.); *V. obscurum* (r.); *V. rotundifolium* (r.); *V. anceps* (r.). Hemiparasites on trees and shrubs, but mostly rare and, on the whole, characteristic of dry and xerophytic scrub. Though the list is given here, many of the rarer ones should probably rather be included with thorn scrub.

SANTALACEÆ.—*Osyridocarpus natalensis*, straggler (f.); *Osyris abyssinica*, shrub (f.).

EUPHORBIACEÆ.—*Euphorbia* spp. See under thorn veld and thorny scrub. The tree *Euphorbias* occasionally come into coast scrub of the mesophytic type, but are not characteristic. *Synadenium arborescens*, shrub (r.); *Noto-buxus natalensis* (591), shrub (r.); *Bridelia micrantha*, tree (l.d.); *Phyllanthus genistoides*, *P. glaucophyllus*, *P. myrtaceus*, *P. tenellus*, herbs or shrubs (f.); *Drypetes* spp.; *Cyclostemon natalensis*, tree (f.); *C. argutus*, tree (a.); *Antidesma venosum* (336), small tree (a.); *Croton sylvaticus*, tree (o.); *C. gratissimus*

shrub or small tree (o.); *Cluytia* spp., undershrubs (a.); *Claoxylon* sp., small tree (r.); *Adenocline* sp., herb in fairly dense shade (a.); *Macaranga capensis*, tree (l.d.); in moist places, *Dalechampia capensis* (515), climber (a.), around outer margin; *Spirostachys africana*, tree (l.a.); *Sapium mannianum*, tree (a.); *Tragia durbanensis*, climber (o.); *T. schlechteri*, climber (o.); *Gelonium africanum*, shrub (r.). This is one of the most important families in coast scrub, including a number of common trees, one (*Macaranga*) often dominant. The trees, however, belong more properly to true forest.

URTICACEÆ.—*Celtis kraussiana* (28), tree (a.); *Trema bracteolata* (356), tree (l.d.); *Chætachme aristata*, shrub or small tree (a.); *Ficus capensis*, tree (l.d.); *F. natalensis*, tree (l.d.); *F. sycomorus*, tree (l.d.), on alluvial mud-flats at river mouths; *F. nekbudu* (l.a.). The figs belong to the early forest stages of the hydrosere. *Urera tenax*, shrub (l.a.); *Pouzolzia parasitica*, shrub (o.); *Australina acuminata*, annual herb (f.), and *Urtica urens*, *Fleurya grossa*, *F. capensis*, herbs with stinging hairs frequent around the margin. Another important family, but the large trees belong rather to high forest.

MYRICACEÆ.—*Myrica conifera*, shrub or small tree (o.).

ORCHIDACEÆ.—The following species are epiphytic: *Ansellia gigantea*, *Polystachya sandersoni*, *Angræcum chiloschistæ*, *A. mystacidii*, *Listrostachys arcuata*, *Mystacidium gerrardi*, *M. millari*, *M. caffrum*, *M. pusillum*, *M. gracile*, *M. filicorne*, all of them rather rare.

The following terrestrial orchids occur in moist or sandy places around the margin: *Calanthe natalensis*, *Eulophia mackenii*, *E. flaccida*, *E. robusta*, *E. barbata*, *E. ensata*, *Lissochilus speciosus*, *L. sandersoni*, *Zeuxine cochlearis* (582), *Platylepis australis*, *Stenoglottis longifolia*, *Habenaria malocophylla*, *Bonatea sandersii*, *B. speciosa*, *Satyrium sphærocarpum*, *Disa polygonoides*, *Corycium nigrescens*, *Disperis stenglossa*, *D. woodii*. They are widely scattered and not

abundant in any one spot. They should all be considered occasional rather than frequent. Other marginal species are listed under vlei vegetation. Any of them occur in moist places around the scrub.

SCITAMINEÆ.—*Kæmpferia natalensis*, herb (r.); *Strelitzia augusta*, small tree (up to 18 ft.) (a. or l.d.), forms consociates in open glades (Pl. XXIII, fig. 2).

HÆMODOURACEÆ.—*Sansevieria thyrsiflora*, fibrous undershrub (a.) in light shade around the margin.

IRIDEEÆ.—*Moræa iridioides*, creeping rhizome (o.); *Lapeyrousia cruenta* (54), corm (f.); *Tritonia lineata*, corm (f.); *Crocasmia aurea* (519), corm (a.); *Acidanthera platypetala*, corm (f.); *Gladiolus papilio* (528), corm (o.); *G. rachidiflorus*, corm, around the margin, together with many of the vlei species.

AMARYLLIDACEÆ.—*Clivia nobilis* (r.), *C. miniata* (503), (a.) in light shade, not bulbous; *Hæmanthus albomaculatus* (548), bulb (f.); *H. natalensis*, bulb (f.); *H. puniceus* var. *membranaceus*, bulb (o.), *Crinum longifolium*, bulb, in moist places around the margin, together with vlei species.

DIOSCORACEÆ.—*Dioscorea malifolia* (317); *D. multiloba*; *D. diversifolia*; *D. undatiloba*; *D. dregeana*; *D. crinita* (17); all with tuberous hypogæous rootstock and slender twining stems (f.). *Testudinaria sylvatica*, large half epigæous, deeply areolated tuber, 2–3 ft. in diameter, and slender twining stems, rather rare, in rocky places.

LILIACEÆ.—*Smilax kraussiana* (339), climber (r.); *Asparagus plumosus*, *A. declinatus*, *A. subulatus*, *A. asiaticus*, *A. africanus*, *A. saundersiæ*, *A. falcatus* (a.), *A. medioloides*, *A. sarmentosus*, *A. æthiopicus* var. *natalensis*, woody climbers with prickles (a.); *Draecæna hookeriana*, small undershrub, simple stem (a.); *Behnia reticulata*, much branched shrub (a.); *Kniphofia pauciflora*, *K. laxiflora*, *K. natalensis* (305), *K. rooperi* (540), bulbous marginal plants (o.); *Aloe thraskii* (l.d.); in open spaces near the sea; *Gloriosa virescens*,

climber (o.), *Sandersonia aurantiaca* (o.) and *Littonia modesta* (o.), both with tuberous rootstocks.

COMMELINACEÆ.—*Commelina nudiflora*, *C. benghalensis*, *C. africana*, *C. krebsiana*, *C. eckloniana*, *C. gerrardi*, *Aneilema æquinoctiale* (284), *A. dregeanum*, *A. sinicum*, *Coleotrype natalensis* (48), *Cyanotis nodiflora*, *Floscopa glomerata*, weak, straggling, succulent annual herbs, common among the grasses and shrubs of the marginal zone. Most of them are also common as weeds.

FLAGELLARIACEÆ.—*Flagellaria guineensis*, tall, herbaceous climber, with tendril-tipped leaves (a.).

PALMÆ.—*Phœnix reclinata* (l.a.).

AROIDEÆ.—*Stylochiton natalense* (207), (r.); *Richardia africana* (*Zantedeschia æthiopica*), common in moist places.

CYPERACEÆ.—Many of the vlei species are common along the margins. *Cyperus albobstriatus* is abundant in fairly dense shade, forming larger societies.

GRAMINEÆ.—In addition to those already dealt with, *Panicum laticomum*, *Oplismenus africanus*, *Potamophila prehensilis* penetrate through the scrub in dense shade.

The 700 odd species, which can be referred to this type, include about half the total number recorded for the coast belt. The majority, however, are marginal species, since the conditions of light or shade, moisture or dryness, vary very much in this zone. If we exclude the grasses of the marginal belt, the percentages of species belonging to different growth-forms in the scrub as a whole work out approximately as follows: climbers 24 per cent.; trees (including the forest species as they occur in the scrub) 15 per cent.; small trees or shrubs (species variable in growth-form) 8 per cent.; shrubs 17 per cent.; undershrubs 10 per cent.; herbs 21 per cent.; epiphytes 2 per cent.; parasites 3 per cent.

The climbers are extremely abundant, both individually and in number of species. They cover the pioneer shrubs and trees around the margins and increase the shade, thus decreas-

ing the number of undershrubs and herbs and ousting all the light-demanders. Only the seedlings of such species as can withstand dense shade can grow underneath. There are over 160 climbing or rambling species altogether. See particularly the families Ranunculaceæ, Anonaceæ, Menispermaceæ, Capparideæ, Malpighiaceæ, Ampelideæ, Connaraceæ, Leguminosæ, Rosaceæ, Passifloraceæ, Cucurbitaceæ, Compositæ, Plumbagineæ, Oleaceæ, Apocynaceæ, Asclepiadaceæ, Convolvulaceæ, Solanaceæ, Bignoniaceæ, Acanthaceæ, Phytolaccaceæ, Euphorbiaceæ, Liliaceæ, Flagellariaceæ, Gramineæ, in the above list.

The trees in the scrub, though species which grow much taller in true forest are included, rarely exceed 30 ft. in height. The extremely mixed character of the coast scrub has already been emphasised. None of the tree species can be described as more than locally dominant—in fact pure dominance, except over very small patches, hardly occurs. This is partly due to the unstable transitional nature of the scrub, but it appears to be a feature of tropical vegetation everywhere. Thus Wallace,¹ in describing the forests of the tropics, remarks: "Among their best distinguishing features are the variety of forms and species which everywhere meet and grow side by side, and the extent to which parasites, epiphytes and creepers fill up every available station with peculiar modes of life. If the traveller notices a particular species and wishes to find more like it, he may often turn his eyes in vain in every direction. Trees of varied forms, dimensions and colours are around him, but he rarely sees one of them repeated. Time after time he goes towards a tree, which looks like the one he seeks, but a closer examination proves it to be distinct. He may, at length, perhaps, meet with a second specimen half a mile off, or may fail altogether, till on another occasion he stumbles on one by accident." These remarks, only to a less degree, apply also to the Natal coast belt scrub. In its general ecological characters,

¹ Wallace, A. R., 'Tropical Nature and other Essays,' London, 1878.

therefore, as well as in its floristic composition, it shows marked tropical affinities. Wallace goes on to suggest that the mixed character of tropical forest is due to the extreme equability and permanence of the climate. "Every form of vegetation has become alike adapted to its genial heat and ample moisture, which has probably changed little throughout geological periods; and the never-ceasing struggle for existence between the various species in the same area has resulted in a nice balance of organic forces, which gives the advantage now to one, now to another species, and prevents any one type of vegetation from monopolising territory to the exclusion of the rest."

This doubtful explanation might be applied (if it applies at all) rather to explain the mixed character of climax forest, but the scrub is still more mixed, and this is due largely to the fact that it is not a climax, but an intermediate type, wherein competition between the various species is very keen, and only lapse of time is necessary for the suppression of many of them. Fewer species can act as pioneers, so the very earliest stages often contain fairly large and relatively pure consocieties, which gradually become more mixed by the invasion of other species.

In addition to the large number of climbing plants already referred to, including woody lianes with watch-spring tendrils (*Dalbergias*), there are other general features illustrating the subtropical nature of coast scrub. The species are all ever-green of course, even those with a wider range, which may be regularly deciduous on the Drakensberg. The leaves are either fairly large, rather thick, smooth, symmetrical and glossy, or much subdivided, often finely pinnate—all characters which agree with tropical forest. Epiphytes are not very abundant, but a dozen or more occur (see under *Orchidaceæ*, *Scrophulariaceæ*, *Piperaceæ*). Parasites are about equally represented (see under *Loranthaceæ*, *Convolvulaceæ*, *Scrophulariaceæ*). Cauliflory (stem-flowering) is seen in *Halleria lucida* and *Rawsonia lucida*, *Ficus capensis*, *F. sycomorus*, *Schotia brachypetala*, *Cyclostemon*

natalensis, the flowers being adapted for pollination by butterflies which frequent the shady places inside the scrub.

Coast scrub is capable of developing and does develop over practically the whole coast belt, except in the drier, hotter situations, where thorn scrub is the climax type. Grassveld always gives way to it, as it in turn does to forest. The fact that the existing scrub is so patchy is due entirely to man's influence in clearing the ground for the cultivation of sugar-cane. Coast scrub without essential change occurs also on the sand-dunes, where it progresses towards psammophilous bush or forest. Fuller details of the plant succession and further reference to the component species will be given later, when forest is dealt with.

8. MANGROVE VEGETATION.

This type develops on the mud-flats at the river estuaries. One of the best examples of it occurs around Durban Bay, into which the Umbilo and Umhlatusan empty their waters, but it also occurs further south along the other rivers of Natal and the Transkei as far as the Kogha river mouth, south of lat. 32°. At Durban the White Mangrove, *Avicennia officinalis* (Verbenaceæ) (Pl. XXII, fig. 1), is dominant around the head of the Bay on the Congella and Umbilo flats. The trees grow isolated or in clumps in the mud, their roots being covered by salt water at high tide. Numerous breathing-roots grow vertically upwards, often through clumps of *Salicornia* and *Chenolea*, the pioneer species already described. The other two mangroves at Durban are *Rhizophora mucronata* and *Bruguiera gymnorhiza* (Rhizophoreæ), both of them somewhat rarer and growing further out along the shores of the Bay. The succession here is very simple. The roots of the mangroves collect and hold the mud brought down by the rivers. The level of the mud-flats consequently rises until the surface is beyond the reach of the salt water. The rivers continue to flood the flats, and the water becomes less and less salt. As soon as it becomes

quite fresh the mangroves give way to vlel types, which are soon invaded by hygrophilous trees, e. g. *Eugenia cordata*, *Voacanga dregei*, *Hibiscus tiliaceus* (Pl. XXV, fig. 2).

The interest of the mangrove type lies not so much in the ground it occupies—for it is quite subordinate to other coast bush in point of size—but in its being a southern outlier of the great mangrove flora which lines the low-lying shores of the tropics throughout the world. Northwards from Zululand through Portuguese East Africa it becomes a very important type, extending inland for many miles along the rivers. In addition to the more hardy southern representatives, many other species occur there—e. g. *Cerriops candoliana*, *Carapa moluccensis* (*Xylocarpus granatum*), *Lumnitzera racemosa*, *Sonneratia acida*, *Heritiera littoralis*, with the fern *Acrostichum aureum*, as in Natal, a common companion.

9. BARRINGTONIA CONSOCIES.

This type is also much better developed in the tropics, and has been dealt with by several ecologists, including Schimper¹ for India and Whitford² for the Philippines. In Portuguese East Africa, according to a note in the 'Flora of Tropical Africa' (Oliver), *Barringtonia racemosa* "lines the Rovuma River (Mosambique) for twenty miles (Kirk)." In Natal *Barringtonia consocies* occur at the river mouths above the lagoons and mud-flats in wet sandy soil, where the water is not brackish. *Barringtonia racemosa* is dominant, but other species which together form distinct associates further inland are commonly associated with it, e. g. *Eugenia cordata* and *Voacanga dregei*, with climbing *Ipomæas* and many other subordinate hygrophilous scrub species.

Hibiscus tiliaceus is a very constant associate never

¹ Schimper, A. F. N., 'Die Indo-malayische Strand-flora,' 1891.

² Whitford, H. N., "The Vegetation of the Lamas Forest Reserve," 'Philip. Journ. of Science,' i, 373, 1906.

occurring very far from the sea, in fact the type in most places might be described as a *Barringtonia-Hibiscus* associates.

10. HYGROPHILOUS BUSH.

(*umDoni* or Waterboom associates, Pl. XXV, fig. 2.)

The earliest stages of the succession along the stream banks, vleis, and in or near water generally, have already been dealt with. Forest species are often very early arrivals. Their fruits are usually eaten by birds, which congregate in such moist situations, thus bringing the seeds where they can most easily germinate. These species soon grow tall enough to oust the earlier reeds and sedges, and a very distinct type of bush or forest becomes established. The Waterboom or *umDoni*, *Eugenia cordata*, is often dominant and always characteristic. It is associated with other species of about equal importance, any one of which may be dominant, *Voacanga dregei*, *Rauwolfia natalensis*, *Ficus capensis*, *F. natalensis*, *Macaranga capensis*. Other tree or shrub species are not quite so important. *Trema bracteolata*, *Mæsa lanceolata*, *Combretum kraussii*, *C. salicifolium*, *Pittosporum viridiflorum*, *Celtis kraussiana* (28), *Myrica conifera*, *Myrsine melanophleos*, *Acacia* spp., *Erythrina caffra*, *Rhamnus zeyheri*, *Bridelia micrantha*, *Antidesma venosum*, *Croton sylvaticus*, *Sapium mannianum*, *Albizzia fastigiata*, *Clerodendron glabrum*, *Cussonia umbellifera*, *Protorhus longifolia*, *Cassipourea verticillata*. Many of these species grow very tall, and when other coast forest is destroyed by clearing operations, being in somewhat inaccessible positions or not being of use for timber they are often left standing. Isolated patches of apparently primeval forest along the stream banks at the present time really represent this early stage of forest development and are not to be taken as typical of coast forest as a whole.

Such hygrophilous bush occurs all over the coast belt.

Plate XXV shows it developing after *Phragmites* which follows after *Avicennia* near Durban Bay. It is common along all the streams.

Other forest species invade it or grow up around its moist margins, the seeds once more being brought by birds. The hygrophilous bush thus serves as the base of colonisation for the intervening ridges between the streams, as explained later. The climbing plants, undershrubs and herbs occurring in such hygrophilous bush are the same as those found in the coast scrub already described.

11. PSAMMOPHILOUS BUSH.

(Pl. XXII, figs. 1 and 2; Pl. XXIII, fig. 1.)

This occurs on the fixed sand-dunes, which line practically the whole coast except at the river mouths, and vary in height from 50 to 200 ft., and in width from a few yards to half a mile. The dominant trees grow to a height of from 30 to 40 ft. The early stages of the succession have again already been dealt with.

(a) The strand vegetation forms the initial stages.

(b) The transitional marginal belt on the side next the sea has also been described.

(c) Following on this, there are several somewhat halophytic varieties of scrub (Pl. XXII). Even though the majority of the species are common to coast scrub generally, on the sand-dunes they tend to show differences in growth-form and leaf-succulence, which, taken in the aggregate, give the sand-dune scrub a slightly different physiognomic appearance. The following are characteristic species: *Aloe thraskii* (common in open spaces), *Chironia baccifera*, *Carissa grandiflora* (14), *Eugenia capensis*, *Cassine albanensis*, *Celastrus procumbens*, *C. angularis*, *Canavalia bonariensis*, *Bauhinia tomentosa* (399), *Cynanchum natalitium*, *C. capense*, *C. schistoglossum*, *C. obtusifolium*, *Turraea obtusifolia*, *Passerina filiformis*, *Osteospermum moniliferum* (55), *Capparis zeyheri* (214),

Grewia occidentalis (210), *Combretum bracteosum* (77), *Pavetta obovata* (313), *Mitrostigma axillare*, *Rhus natalensis* with *Dracæna hookeriana*, *Hæmanthus albomaculatus*, *Disperis woodii*, *Acidanthera brevicollis*, *Gloriosa virescens*, *Harveya squamosa*, and the fern *Polypodium phymatodes* as herbaceous undergrowth.

(d) Approaching the climax in many places *Strelitzia augusta* is dominant, forming consocieties (Pl. XXIII, fig. 2).

(e) At many other places there is a *Strelitzia*-*Osteospermum* consociety—*Strelitzia augusta* with *Osteospermum moniliferum*.

(f) In some of the more open glades, the palm, *Phoenix reclinata*, is fairly common, usually associated with *Strychnos spinosa*.

(g) Typical sand-dune climax bush has the following composition, the species being named roughly in the order of their abundance: *Mimusops caffra*, *Euclea natalensis*, *Schmidelia erosa*, *Euclea undulata*, *Brachylæna discolor*, *Dovyalis celastroides*, *Sapindus oblongifolius*, *Xanthoxylon capense*, *Tarchonanthus camphoratus*, *Elæodendron velutinum*, *Apodytes dimidiata*, *Brachylæna elliptica*, *Grewia caffra*, *Olea capensis*, *O. woodiana*, *Cordia caffra*, *Sideroxylon inerme*, *Dovyalis zizyphoides*, *Tricalysia lanceolata*, *Erythrina caffra*, *Grewia occidentalis*, *Pterocelastrus* sp., *Ekebergia meyeri*, *E. capensis*, *Psychotria capensis*.

Lianes are very numerous, practically all the coast scrub species being found. The result is a tangled impenetrable growth which throws a very dense shade. There is very little herbaceous undergrowth in climax sand-dune bush. The trees are very deep rooted and blow-outs are infrequent except on the side next the sea, where the climax type does not occur. The main dunes have been fixed for a long period of time.

12. COAST FOREST.

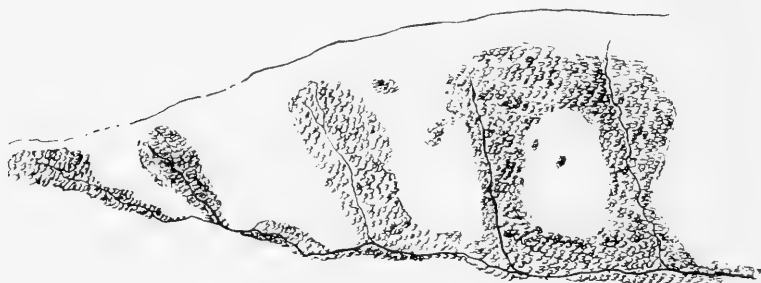
(Pl. XXVI, figs. 1 and 2.)

This represents the chief climax stage in the plant succession on the coast belt. In places, where thorn scrub is dominant, the climate is too hot and dry to permit of forest development, and in other places, though forest species of trees are dominant, they are unable to develop into true high forest, but remain dwarfed so as to form scrub like that already described. Such scrub forest is, of course, also climax, but it is probable that this state of affairs has, to a large extent, been caused by the extensive destruction of forest and scrub from all the surrounding country. Fourcade, in his 'Report on the Natal Forests,' published as a government blue book nearly thirty years ago, says, "The coast forest is still extensive, but much of it has been cleared for planting. Nearly the whole of the cultivated land in the coast districts consists of cleared bush ground. This extensive denudation is said by old settlers to have somewhat altered the climate, causing a greater aridity and more irregularity in the weather. Yellow-wood and wagon-wood were formerly cut in many of the coast forests, but few good timber trees are now left." That was written at a time when the sugar industry was only about one-sixth as extensive as it is now. (In 1894, 19,369 tons of sugar were produced, while in 1916 the amount was 114,500 tons, and the acreage under cane had increased from 26,000 acres in 1892 to 163,000 acres in 1916. This year, 1919, the estimated yield is 160,000 tons.) Over practically the whole coast belt from Port Shepstone to Zululand, within easy reach of the railway, one sees nothing but sugar cane, except in occasional patches. The village commonages have often been left untouched, and much of the native locations have not been planted with cane, but these have usually been otherwise interfered with.

One of the best examples of coast forest is at the same time the most accessible of all—the "Stella Bush" on the Durban Berea. In Bulwer Park fine original forest trees have been

left standing, the undergrowth only being cut away. Towards Congella and Umbilo the forest deteriorates into scrub. All these places can be reached in a few minutes by tramway from Durban. Near Port Shepstone there is also a representative patch of primeval forest containing some fine specimens of the Natal mahogany, *Trichilia emetica*. Further inland, away from the coastal railway, there are frequent small patches of scrub and forest, usually in somewhat inaccessible situations. Enough remains to show that the succession in coast forest is similar in its main features to that in the midlands and Drakensberg.

TEXT-FIG. 2.



Succession in forest in Natal.

It was pointed out in a former paper¹ that in the Drakensberg a zone of scrub preceded the forest. Further details were given by Henkel.² The mode of succession appears to be essentially the same for all South African forest, and is illustrated diagrammatically in text-fig. 2. It should be noted that the majority of the tree species are distributed by birds and other animals. These transport the seeds along the stream banks and in such moist situations the forest succession is initiated. The Waterboom associates (hygrophilous bush) is frequently the first stage of it on the coast belt. As long as the bush is confined to the stream bank, *Eugenia cordata*,

¹ Bews, J. W., "The Plant Ecology of the Drakensberg Range," 'Ann. of Natal Museum,' vol. iii, pt. 3, 1917.

² Henkel, J. S., "Forest Progress in the Drakensberg," 'S.A. Journ. of Sci.,' December, 1916.

Voacanga dregei, *Ficus* spp., etc., remain dominant, but soon other species arrive and scrub begins to develop around the margins. This gradually advances up the slopes, and between parallel tributaries the intervening ridges gradually get covered. Forest follows the zone of scrub. Islands of grass veld may be found surrounded by scrub and in a wider circle by forest (text-fig. 2).¹ The advance has been from two parallel streams on opposite sides of the island, and sufficient time has not elapsed to cover completely the intervening ground. A transect taken across a forest-clad valley shows the oldest trees at the valley bottom, and all the stages of the succession from the initial to the climax are shown along such a transect. The succession is most clearly marked on rather drier ridges, for there it takes some considerable time for scrub to give way to forest. In moister situations, and especially near the streams themselves, the early scrub stages are more transitory and the tree species may appear before the shrubs—the type of succession seen in tree veld. The drier ridges, however, can only be conquered by pioneer scrub composed of somewhat xerophytic light-demanding shrubs and small trees, which prepare the way for the taller-growing, more hygrophilous, more shade-loving forest species. The ultimate stages are dominated by species which are shade-bearers in their early stages and light-bearers at maturity. They themselves throw dense shade, which easily kills out the seedlings of competitors and in many cases even their own seedlings. The forest has then reached a stable climax condition at which it remains, until the death of old trees begins to leave gaps which admit light and give an opportunity for the seedlings of such species as show the best powers of regeneration to grow up. A succession of extra dry years often leads to many old trees dying at the same time, and at such times fires are especially dangerous. As a rule the forest is too moist for wholesale destruction by fire, but if it contains much dead wood a fire may sweep through.

Regeneration in the open spaces of a forest is not always

¹ Cf. Henkel, J. S., loc. cit.

found to be from the seedlings of the dominant surrounding trees. Though these may produce abundance of seed, there are numerous insect-pests which, during the stationary climax period, often become so abundant that all the seeds of the dominant species are attacked and none of them are able to germinate. Some of the sub-dominant species may show signs of gradually supplanting the dominant ones, owing to the influence of such animal agencies, and it is particularly interesting to find that the animal influence can thus prove more potent than the climatic in leading to changes in the climax phase. In other words, the climax type of vegetation may change without any change in the climate.

All this applies to South African forest as a whole, but very little (if any) of the coast-belt forest has really reached such a climax stage. On the whole it is rather mixed in composition and generally low, few of the trees being more than 60 feet high.

The tallest trees, named roughly in the order of their importance, are: *Protorhus longifolia*, *Albizzia fastigiata*, *Rhus lævigata*, *Macaranga capensis* (in moister situations), *Millettia caffra*, *Trichilia emetica*, *Cussonia umbellifera*, *Calodendron capense*, *Toddalia lanceolata*, *Celtis kraussiana*, *Harpephyllum caffrum*, *Cryptocarya latifolia*, *Pygeum africanum*, *Cyclostemon argutus*, *Ekebergia meyeri*, *Myrsine melanophleos*, *Strychnos gerrardi*, *S. atherstonei*, *S. henningsii*, *Cassipourea verticillata*, *Elæodendron croceum*, *Erythrina caffra*, *Ptæroxylon utile*, and rarely the Yellow-wood, *Podocarpus elongata*, but in all the moister situations the hygrophilous type already described may retain dominance, and the component species, *Eugenia cordata*, *Macaranga capensis*, *Rauwolfia natalensis*, *Voacanga dregei*, *Ficus capensis*, *F. natalensis*, grow to a very large size. The more useful timbers like the Yellow-wood may, as Fourcade suggests, at one time have been more abundant. Specimens of it are still to be seen in the Albert Park, Durban, near the sea.

Smaller trees belonging more properly to the scrub are often mixed with the above, but not, of course, dominant, e.g. *Schmidelia monophylla*, *Clausena inæqualis*, *Chætachme aristata*, *Elæodendron capense*, *E. velutinum*, *E. sphærophyllum*, *Bridelia micrantha*, *Apodytes dimidiata*, *Scutia commersoni*, *Baphia racemosa*, *Antidesma venosum*, *Trimeria grandifolia*, *Spirostachys africana*, *Sapium mannianum*, *Peddiea africana*, *Clerodendron glabrum*, *Grewia occidentalis*, *Schotia brachypetala*, *Xanthoxylon capense*, *Celastrus acuminatus*, *C. buxifolius*, *C. undatus*, *Sapindus oblongifolius*, *Chrysophyllum natalense*, *Mimusops obovata*, *M. caffra*, *Euclea lanceolata*, *E. natalensis*, *Erythroxylon emarginatum*, *E. pictum*, *Scolopia zeyheri*, *Oncoba kraussiana*, *Dovyalis zizyphoides*, *D. celastroides*, *Aberia caffra*, *Garcinia gerrardi*, *Cola natalensis*, *Zizyphus mucronata*, *Combretum gueinzii*, *C. erythrophyllum*, *Cussonia spicata*, *C. natalensis*, various Rubiaceous trees (see under scrub), *Royena lucida*, *Maba natalensis*, *Olea verrucosa*, *Schrebera saundersiæ*, *Acocanthera venenata*, *Cordia caffra*, *Ehretia hottentotica*, *Halleria lucida*, *Cryptocarya woodii*, *Cyclostemon natalensis*, *Croton gratissimus*.

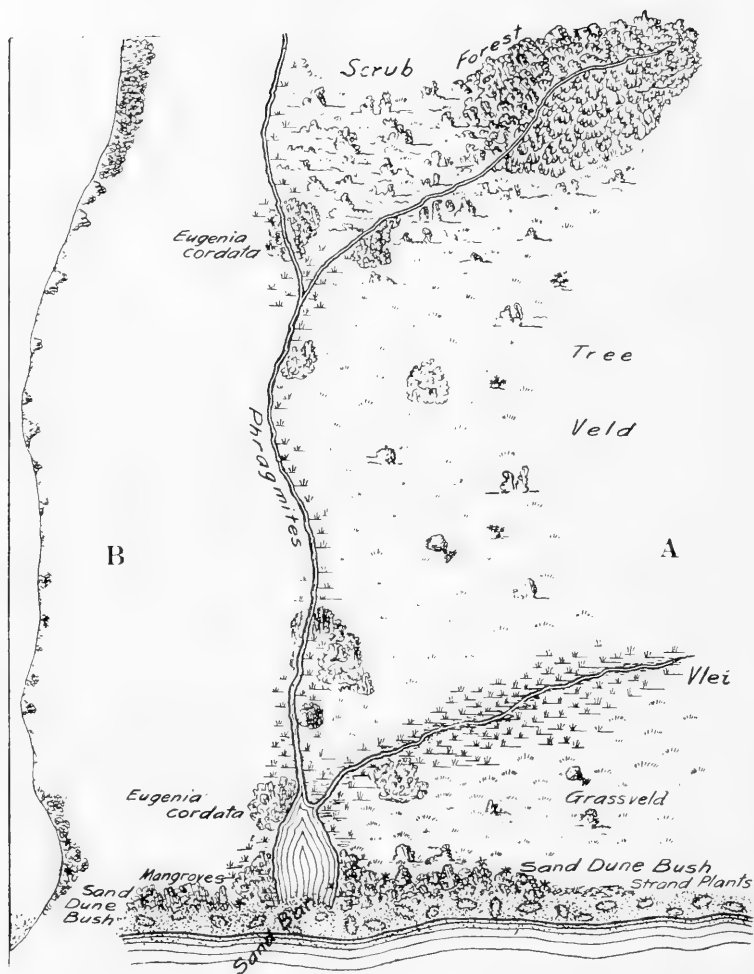
The lianes characteristic of the scrub zone penetrate through the forest, many of them climbing to the tops of the highest trees, but they are not so abundant. The epiphytes, parasites, undershrubs and herbs are also as described for scrub.

It will be seen, therefore, that the essential point in which high forest differs from the scrub which it replaces is simply in the dominance of the tall timber trees.

VI. GENERAL SUMMARY.

The low-lying coast belt of Natal is ecologically a fairly uniform subtropical region. The topography is practically independent of the geological structure, which is described in outline. Numerous rivers at right angles to the coast-line

TEXT-FIG. 3.



A. The distribution of various types of plant community in the neighbourhood of a typical river mouth on the Natal coast belt. B. Typical section.

cut deeply into the general surface. By a recent downward movement of the continent the river mouths have been "drowned." The subsidence probably exceeded 150 ft. As a result extensive alluvial flats have been formed at the river mouths. The whole of the actual coast-line itself is covered by a mantle of blown sand to a distance of from half a mile to two or three miles from the shore. Close to the sea the sand-dunes are covered by psammophilous bush.

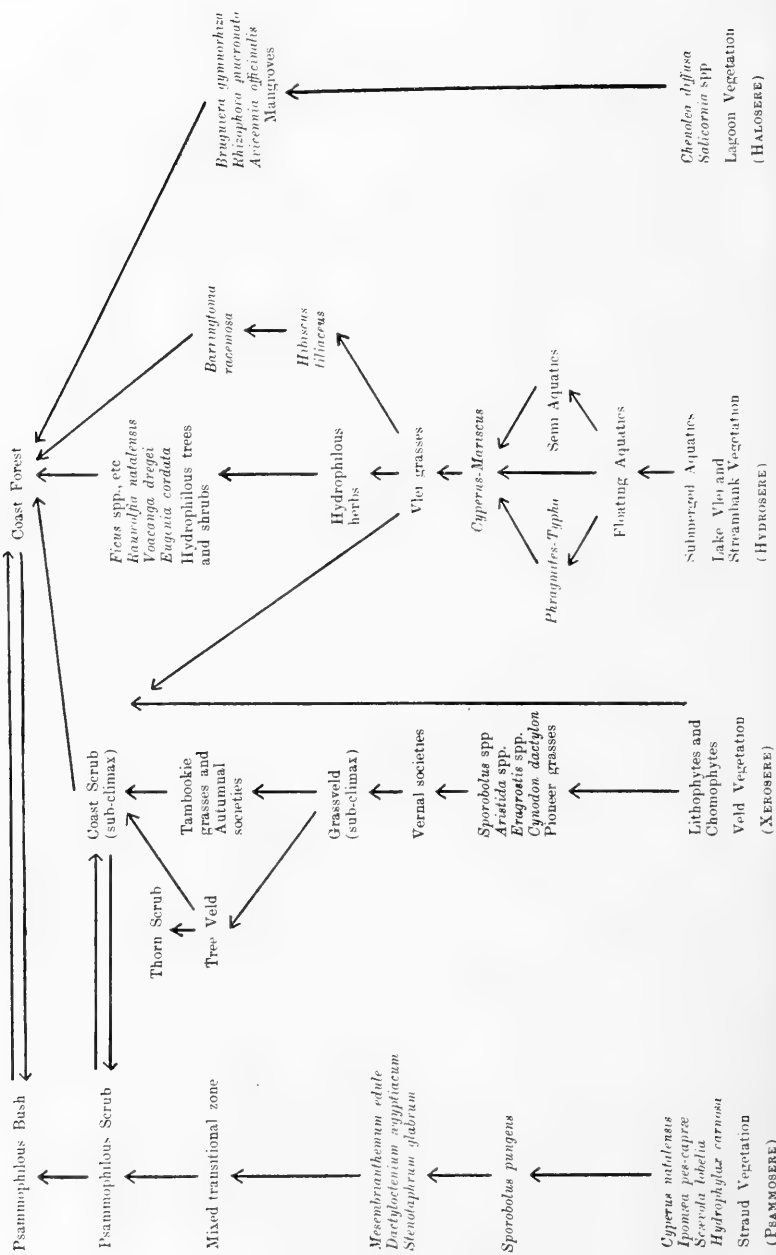
There is little variation in the climatic conditions, most parts being warm and humid with a rainfall of about 40 in., the greater portion of which falls in the hot summer season. In some parts there are drier conditions, with a greater range of temperature and more exposure to dry, hot winds—a difference reflected in the dominance of a thornveld type of vegetation. Frosts are absent or rare over the whole coast-belt.

A floristic analysis of the vegetation shows that about 86 per cent. of the genera and 36 per cent. of the species are tropical. The more temperate species and the species with a wider, general distribution appear early in the succession; as succession advances the vegetation becomes more and more tropical and the species tend to have a more restricted range.

The various plant communities are arranged in the order of the plant succession. The typical distribution of the chief ones near a river mouth is illustrated in text-fig. 3. The actual river mouth itself is completely closed by a sand-bar across which one can walk. Periodically, however, the river, assisted by exceptionally high tides, cuts through such a sand-bar and the lagoon behind is drained out. At all other times the water has to drain through the sand-bar. A section through the plan is given at the left-hand side of the text-figure.

The plant succession and the relationship between the different plant communities can best be summarised graphically, as is done in text-fig. 4. The climax type for most of the coast-belt is bush or forest, but in some of the drier parts thorny scrub is the final stage of the succession.

TEXT-FIG. 4.



VII.—LIST OF ZULU PLANT NAMES.¹

isAmuyisane, <i>Paspalum</i> <i>scrobiculatum</i> .	umBengele, <i>Trema bracteolata</i> .
<i>Spermacoce</i> <i>natalensis</i> .	<i>Cussonia umbellifera</i> .
sAndhla-ka-inkosikasi, <i>Jasminum</i> <i>multipartitum</i> .	uBenhle, <i>Gazania longiscapa</i> .
isAnyana, <i>Tricalysia lanceolata</i> .	uBenyane, <i>Oplismenus africanus</i> .
umBaba, <i>Calodendron capense</i> .	Beta umtunzi, <i>Carissa arduina</i> .
imBabazane, <i>Urtica urens</i> .	imBewu, any kind of seed.
uBabe, <i>Panicum laevifolium</i> .	amaBibi, weeds.
<i>P. maximum</i> .	imBilo, <i>Pterocarpus erinaceus</i> .
umBalele, <i>Synadenium</i> <i>arborescens</i> .	umBimbane, <i>Eragrostis brizoides</i> .
umBambalele, <i>Oplismenus</i> <i>africanus</i> .	isiBinda, <i>Garcinia gerrardi</i> .
umBambangwe, <i>Chaetachme</i> <i>aristata</i> .	i(li)Binini, <i>Embelia kraussii</i> .
umBamatsheni, <i>Erythroxylon</i> <i>pictum</i> .	umBinza, <i>Halleria lucida</i> .
umBanda, <i>Strychnos atherstonei</i> .	iBiqongo, <i>Psychotria capensis</i> .
isiBanda, <i>Rhus laevigata</i> .	uBobo, <i>Entada natalensis</i> .
isiBangamlota, <i>Antidesma</i> <i>venosum</i> .	<i>Xanthoxylon capense</i> .
umBangandhlala, <i>Heteromorpha</i> <i>arborescens</i> .	<i>Acacia kraussiana</i> .
umBangazi, <i>Albizzia fastigiata</i> .	umBofanyamagone, <i>Elaeodendron</i> <i>kraussianum</i> .
uBani, <i>Claoxylon capense</i> .	Bogozembe, <i>Urera tenax</i> .
<i>Agapanthus umbellatus</i> .	umBomane, <i>Isoglossa woodii</i> .
uBatini (uBatini), <i>Trema</i> <i>bracteolata</i> .	umBomvane, <i>Elaeodendron</i> <i>croceum</i> .
amaBele, <i>Andropogon sorghum</i> var. <i>usorum</i> .	<i>Pleurostylia</i> <i>capensis</i> .
i(li)Belelendhlovu, <i>Kigelia</i> <i>pinnata</i> .	<i>Ochna arborea</i> .
	<i>Eugenia zeyheri</i> .
	umBondi, <i>Combretum spp.</i>
	umBondwe, <i>Plectranthus</i> <i>esculentus</i> .
	umBonemfane, <i>Plectronia obovata</i> .
	imBongani, <i>Aristida junciformis</i> .
	i(li)Bontsi, <i>Salacia alternifolia</i> .
	uBoqo, <i>Ipomœa ovata</i> .
	iBoqo, <i>Barringtonia racemosa</i> .

¹ In compiling the list I have been greatly assisted by Rev. A. T. Bryant's works, "Zulu Medicine and Medicine Men," 'Ann. Natal Museum,' ii, 1, 1909, and 'A Zulu-English Dictionary,' 1905. I have also had the opportunity of consulting a manuscript list compiled by Mr. J. S. Henkel, to whom my warmest thanks are due.

- Bovati or Bomvati, *Oxyanthus gerrardi*.
- iBoza, *Iboza riparia*.
- umBozane, *Toddalia lanceolata*.
- umBotane, *T. lanceolata*.
- isiBubu, *Celastrus buxifolius*.
- uBubu, *Choristylis rhamnoides*.
- uBubupu, *Helinus ovata*.
- iBucu, *Bulbine natalensis*.
- imBufa, *Zizyphus mucronata*.
- uBuku, *Oncinotis inandensis*.
- umBulunyati, *Osyris abyssinica*.
- i(li)Bunda, *Dombeya natalensis*.
- umBungane, *Chloris petraea*.
- isiBupu, *Celastrus buxifolius*.
- uBupupu, *Ilex capensis*.
- isiBusana, *Andropogon filipendulus*.
- imButane, *A. pertusus*.
- uButlungubenyoka, *Acocanthera spectabilis*.
- imBuya, *Amarantus* spp.
- inCa (grass generally).
- Cabazane, *Gerbera kraussii*.
- umCabegazane, *Trema bracteolata*.
- umCalatole, *Faurea saligna*.
- umCandotambo, *Schmidelia decipiens*.
- inCani, *Calpurnia* sp.
- umCaloti, *Strychnos henningsii*.
- isiCatankobu, *Gardenia thunbergii*.
- Rinorea ardisæfolia*.
- Gardenia rothmanni*.
- inCathucathu, *Hibiscus surattensis*.
- uCebe, *Andropogon amplexans*.
- umCele, *Ehretia hottentottica*.
- iCena, *Aloe saponaria*.
- i(li)Cibo, *Curtisea faginea*.
- Grewia* sp.
- i(li)Cimamlilo, *Pentanisia variabilis*.
- inCinci, *Bridelia micrantha*.
- iCita, *Scilla kraussii*.
- iCitshumlilo, *Pentanisia variabilis*.
- inClabibi, *Leucosidea sericea* (imKlabibi).
- Cnandana, *Royena villosa*.
- umCobegazane, *Trema bracteolata*.
- inCohiba, *Asclepias* sp.
- umCqabi, *Cryptocarya myrtifolia*.
- umCutunga, *Cryptocarya* spp.
- umCutungwa, *Cryptocarya woodii*.
- umCwili, *Leonotis ovata*.
- umDabu, *Elephantorrhiza burchellii*.
- umDabeka, *Erythroxylon monogynum*.
- umDakane, *Apodytes dimidiata*.
- inDalu, *Greyia sutherlandi*.
- iliDambisa, *Senecio concolor*.
- umDanghan, *Celastrus albus*.
- inDawo, *Cyperus esculentus*.
- uDekane, *Vitis hypoleuca*.
- isiDende, *Mæsa lanceolata*.
- umDhlebe, *Synadenium arborescens*.
- umDhlesa, *Tricalysia lanceolata*.
- umDhlunye, *Ochna arborea*.
- Rawsonia lucida*.
- Dhlula mazembe, *Phyllanthus amapondensis*.
- isiDikili, *Lasiosiphon meisnerianus*.
- umDidi, *Phytica paniculata*.
- iDlebelendhlovu, *Trimeria grandifolia*.
- iliDlelendhlovu, *Homalium* sp.
- umDlonzo, *Mikania capensis*.
- uDlutshana, *Aster asper*.
- inDodennyama, *Royena villosa*.
- inDola, *Gnidia coriacea*.
- inDolo, *Lasiosiphon anthyllioides*.
- iDololenkonyane, *Rumex ecklonianus*.
- umDoni, *Eugenia cordata*.
- umDoni wehlati, *Eugenia gerrardi*.
- umDonqa, *Cerathotheca triloba*.

- umDonqabatwa, *Chenopodium murale*.
 umDubu, *Combretum erythrophyllum*.
 C. salicifolium.
 „ wehlati, *C. kraussii*.
 uDulamuthwa, *Vangueria lasiantha*.
 isiDuli, *Brachylæna elliptica*.
 Brachylæna spp.
 umDuma, *Anastrebe integerrima*.
 Ilex mitis.
 iDumbhi, *Hæmanthus natalensis*.
 Dumizulu, *Pygeum africanum*.
 iDungamuzi, *Euclea lanceolata*.
 E. daphnoides.
 E. natalensis.
 inDungulu, *Kæmpferia natalensis*.
 isiDunwana, *Eugenia gerrardi*.
 umDuse, *Crinum longifolium*.
 isiDwa, *Gladiolus ludwigii*.
 Dwaba, *Popowia caffra*.
 uDwangubane, *Commelina* sp.
 uDwiya, *Hippobromus pauciflorus*.
 ubEndhle, *Gazania longiscapa*.
 Etolonja, *Osteospermum moniliferum*.
 umFana-ka-sihlanjana, *Stylochiton natalensis*.
 umFasha, *Urelytrum squarrosum*.
 imFe, *Andropogon sorghum*, var. *saccharatum*.
 umFeca, *Digitaria sanguinalis*.
 D. tricholænoides.
 umFeyenkomo, *Kiggelaria africana*.
 imFeyenkala, *Dissotis incana*.
 imFeyesele, *D. incana*.
 umFeyesele, *Oxalis* sp.
 isiFici, *Protorhus longifolia*.
 imFingo, *Stangeria paradoxa*.
 umFisane, *Panicum isachne*.
 umFiyo, *Cluytia pulchella*.
 umFomfo, *Cephalanthus natalensis*.
 umFongo-fongo, *Macaranga capensis*.
 Digitaria ternata.
 umFongote, *Kigelia pinnata*.
 isiFuce, *Protorhus longifolia*.
 isiFufufu, *Peddisa africana*.
 uFukuzela, *Becium obovatum*.
 imFulwa, *Ophiocaulon gummifera*.
 umFusamvu, *Pittosporum viridiflorum*.
 maFutumfuleni, *Burchellia capensis*.
 inGabavu, *Trichocladus grandiflorus*.
 uGagane, *Dichrostachys nutans*.
 umGanankawu, *Albizia fastigiata*.
 umGana, *Toddalia lanceolata*.
 umGanu, *Sclerocarya caffra*.
 isiGceba, *Strelitzia augusta*.
 inGcino, *Scilla rigidifolia*.
 inGcolo, *S. rigidifolia*.
 iliGcuma, *Xanthium spinosum*.
 umGeba, *Chilianthus arboreus*.
 uGebelewene, *Rhipsalis cassythæ*.
 Gegeye, *Azima tetracantha*.
 Gibampondo, *Alberta magna*.
 uGibisisela, *Bowiea volubilis*.
 uGoba, *Digitaria diagonalis*.
 uGobanhlovu, *Secamone gerrardi*.
 uGobo, *Gunnera perpensa*.
 isiGobo, *Asparagus* spp.
 uGodidi, *Jatropha hirsuta*.
 umGologoti, *Rhamnus zeyheri*.
 iGololenkama, *Sapindus oblongifolius*.
 isiGolwana, *Burchellia capensis*.
 inGongoni, *Aristida barbicollis*.
 A. junciformis.
 uGonoti, *Flagellaria guineensis*.
 iGontshi, *Ipomæa simplex*.

- um or isiGontswane, *Ficus* sp.
inGqaqabulani, *Smilax kraussiana*.
iGqanse, *Olea laurifolia*.
umGqangqa, *Pleurostyliia capensis*.
inGqapunana, *Scutia commersonii*.
umGqwashu, *Sideroxylon inerme*.
inGqwangane, *Celastrus buxifolius*.
uGqumugqumu, *Physalis peruviana*.
umGulugulu, *Strychnos gerrardi*.
umGwali, *Euclea lanceolata*.
isiGwani wehlati, *Myrsine melanophleos*.
iGwanxe, *Euclea undulata*.
Olea laurifolia.
umGwenye, *Harpephyllum caffrum*.
umGwenyahangula, *Schrebera saundersia*.
umGxama, *Schotia brachypetala*.
inGxanini, *Capparis corymbifera*.
umGxele, *Ehretia hottentottica*.
iGxolo, *Trichilia emetica*.
umHayihayi, *Mimusops caffra*.
umHepuhepu, *Eragrostis curvula*.
iHlaba, *Aloe saponaria*.
umHlaba, *Aloe ferox*.
Weihia madagascarensis.
umHlaba i Boge, *Myrsine africana*.
maHlabakufane, *Croton gratissimum*.
Hlabulele, *Mæsa lanceolata*.
Hlaguti, *Schmidelia monophylla*.
umHlahla (ta), *Antidesma venosum*.
umHlala, *Sideroxylon inerme*.
Strychnos spinosum.
umHlalabenyoni, *Loranthus natalitius*.
umHlalajuba, *Croton sylvaticus*.
umHlala makwaba, *Bridelia micrantha*.
umHlalane, *Cunonia capensis*.
umHlalampunzi, *Sapium mannianum*.
umHlale, *Mimusops* sp.
umHlakela, *Cyclostemon argutus*.
isiHlakoti, *Rhus villosa*.
R. levigata.
umHlakuva, *Ricinus communis*.
umHlambamanzi, *Rauwolfia natalensis*.
Conopharyngia ventricosa.
Gardenia rothmanni.
umHlambahlala, *Scolopia mundii*.
S. ecklonii.
umHlambaluku, *Lotononis corymbosa*.
uHlambihloshane, *Gerbera kraussii*.
umHlambhamas, *Voacanga dregei*.
Conopharyngia ventricosa.
iHlamvu, *Gloriosa virescens*.
umHlanga, *Phragmites communis*.
inHlanhla, *Secamone alpini*.
S. thunbergii.
umHlandhloti, *Albizzia fastigiata*.
inHlangwana, *Putterlickia pyracantha*.
iHlanze, Tree Veld or Scrub.
iHlati, Forest.
isiHlasi, *Polygala* sp.
umHlathalana, *Turraea obtusifolia*.
inHlavubele, *Mæsa lanceolata*.
Hlawi, *Strophanthus capensis*.
Hlazane, *Cassinopsis capensis*.
Ochna arborea.
umHlebe, *Olea laurifolia*.
O. foveolata.

- umHlele, *Ehretia hottentottica*.
 umHlezane, *Ochna arborea*.
 Hlibehlo, *Dombeya rotundifolia*.
 umHloboluku, *Lotononis corymbosa*.
 iHlokoshiyane, *Rhus villosa*.
 iHlolane, *Piper capense*.
 uHlongohlongo, *Setaria sulcata*.
 umHlonishwa, *Psoralea pinnata*.
 isiHlontlo, *Euphorbia* spp. (herbaceous).
 umHlontlo, *Euphorbia* spp. (trees).
 umHlonyane, *Artemisia afra*.
 uHlonyane, *Veronica woodii*.
Hypæstes antennifera.
 umHlonyise, *Secamone gerrardi*.
 uHlosa, *Gnidia ovalifolia*.
 umHloshazana, *Schmidelia melanocarpa*.
 iHlovane, *Calpurnia intrusa*.
 Hlozi, *Cnestis natalensis*.
 umHlulamiti, *Phylica paniculata*.
 umHluluwe, *Dalbergia armata*.
 umHluluozu, *Eugenia owariensis*.
 umHluma, *Rhizophora mucronata*.
 isiHlunga, *Protea hirta*.
 uHlungahlunga, *Vernonia corymbosa*.
 Hlunguti, *Commiphora caryæfolia*.
 umHlungwane, *Aster asper*.
 ubuHlungwane, *Wedelia natalensis*.
 umHluti, *Protorhus longifolia*.
 umHlutiwezingha, *P. longifolia*.
 iHluze, *Schotia brachypetala*.
 umHlwagela, *Cyclostemon argutus*.
 umHlwakele, *C. argutus*.
 umHlwati, *Olea verrucosa*.
 uHlwehlwe, *Xymalos monospora*.
Excæcaria sp.
 umHulana, *Turraea heterophylla*.
 umHuluma, *T. heterophylla*.
 iJalambu, *Ipomæa purpurea*.
I. congesta.
 umJela, *Rauwolfia natalensis*.
 iJingijolo, *Rubus rigidus*.
 umJuluka, *Casiaria junodi*.
 uKaba-ka-umtwan, *Vangueria latifolia*.
 umKahla, *Voacanga dregei*.
 umKahlu, *Conopharyngia elegans*.
 umKakasi, *Erythrina tomentosa*.
Pygeum africanum.
 inKalane, *Aloe* sp. (dwarf).
 isiKali, *Kiggelaria dregeana*.
 umKamba, *Acacia* sp.
 iKambi, medicinal herb of any kind.
 iKambi leziduli, *Cardiospermum helicacabum*.
 umKangala, *Strychnos atherstonei*.
 inKangala, open treeless veld.
 umKangaza, *Gardenia thunbergi*.
 umKangeli, *Strychnos atherstonei*.
 umKatana, *Weihea gerrardi*.
 isiKatankobu, *Gardenia* spp.
Rinorea ardisæfolia.
 inKaza, *Euclea natalensis*.
 umKaza, *Royena lucida*.
 uKedeza, *Pavetta lanceolata*.
 isiKelekehlane, *Crassula rubicunda*.
 uKhalimele, *Rhynchosia* sp.
 iKhambi lamabulawo, *Mesembrianthemum edule*.
 umKhambiba, *Clausena inæqualis*.
 umKhiphampetha, *Calpurnia lasiogynne*.
 umKhokha, *Abrus precatorius*.
 umKhokha wehlati, *Ipomæa ficifolia*.
 isiKholokotho, *Sansevieria thyrsoiflora*.
 umKhovothi, *Chætachme aristata*.

- isiKhubabende, *Indigofera micrantha*.
 umKhuhlu, *Trichilia emetica*.
 umKisiso, *Cussonia umbellifera*.
 umKiwane, *Ficus capensis*.
 Cyclostemon natalensis.
 Erythrina tomentosa.
 iKlolo, *Grewia occidentalis*.
 G. caffra.
 umKoba, *Podocarpus elongata*.
 umKobese, *Nuxia congesta*.
 isiKobo, *Asparagus falcatus*.
 umKoko, *Pygeum africanum*.
 umKokuti, *Elæodendron kraussianum*.
 Celastrus undatus.
 umKokolo, *Dovyalis rhamnoides*.
 isi or umKomakoma, *Cyathea dregei*.
 isiKomane, *C. dregei*.
 inKomankoma, *Nephrodium athamanticum*.
 inKombota, *Chætachme aristata*.
 umKomizo, *Protorhus longifolia*.
 inKomfe, *Hypoxis rooperi*.
 inKonazana, *Alysicarpus rugosus*.
 inKondhlwane, *Helichrysum aureo-nitens*.
 isiKonko, *Digitaria eriantha*.
 inKonkoni, *Aristida barbicollis*.
 A. junciformis.
 umKovati, *Dalbergia armata*.
 iKowe, edible mushroom.
 inKowankowane, poisonous mushroom.
 iKowendhlovu, edible mushroom (largest kind).
 umKuana, *Tricholæna rosea*.
 umKuhlu, *Trichilia emetica*.
 Strychnos gerrardi.
 umKukuze, *Elæodendron kraussianum*.
 uKula, weeds.
 umKumane, *Alberta magna*.
 maKunda, *Curtisea faginea*.
 umKunye, *Milletia sutherlandi*.
 inKunzana, *Emex spinosa*.
 inKunzi, *Bopusia scabra*.
 Olinia cymosa.
 inKwa, *Dioscorea rupicola*.
 umKwakwa, *Strychnos* sp.
 umKwabakwaba, *Erythrina tomentosa*.
 isiKwali, *Vigna triloba*.
 i(li)Kwani, *Cyperus* sp.
 umKwashube, *Cunonia capensis*.
 umKwenkwe, *Pittosporum viridiflorum*.
 inKweza, *Tricalysia floribunda*.
 iLabatheka, *Hypoxis latifolius*.
 umLahlankosi, *Zizyphus mucronata*.
 i(li)Lala, *Hyphæne crinita*.
 uLala, forest margin.
 iLalanyathi, *Grewia occidentalis*.
 umLalume, *Curtisea faginea*.
 Leti, *Gerrardiana foliosa*.
 uLimilwenkomo, *Berkheya debilis*.
 uLimilwenyathi, *B. debilis*.
 iLitye, *Pappea capensis*.
 Loluti, *Cluytia schlechteri*.
 umLolo, *Hibiscus tiliaceus*.
 umLolwa, *H. tiliaceus*.
 Dombeya rotundifolia.
 iLotjanc, *Buddleia salviaefolia*.
 B. pulchella.
 Lovulovu, *Cordia caffra*.
 iLozane, *Tephrosia macropoda*.
 umLulama, *Canonia capensis*.
 Turraea heterophylla.
 uLuncwe, treeless country.
 umLunge, *Antholysa paniculata*.
 u(h)Lusi, *Ficus nekbudu*.
 Luxwezo, *Notobuxus natalensis*.
 umLwalume, *Curtisea faginea*.

- isiNami, *Capparis albitrunca*.
 umNamnami, *Oncoba kraussiana*.
 isiNandi, *Cynodon dactylon*.
 Dactyloctenium
 ægyptiacum.
 Panicum helopus.
 Nanga, *Rawsonia lucida*.
 umNanja, *Eugenia albanensis*.
 Phytolacca stricta.
 umNcaka, *Erythroxylon pictum*.
 i(li)Ncamu, *Othonna natalensis*.
 umNcatyane, *Cryptocarya* sp.
 umNcele, *Andropogon pertusus*.
 A. intermedius.
 umNcongo, *Ficus* sp.
 u(lu)Newe, open treeless country.
 isiNdiyandiya, *Bersama lucens*.
 uNdwendweni, *Eulophia*
 arenaria.
 umNebelele, *Albizzia fastigiata*.
 Heywoodia lucens.
 umuNga, Thorn tree (any kind).
 Acacias and *Dichro-*
 stachys nutans, etc.
 umuNgamanzi, *Acacia caffra*.
 umuNgapunzi, *A. hirtella*.
 Ngai, *Mystroxylon*
 eucleæformis.
 Ngana, *Rhus gueinzii*.
 umNgane, *Buddleia pulchella*.
 umNgqabe, *Encephalartos* sp.
 uNgwalene, *Cluytia pulchella*.
 Ngwele, *Rhus* sp.
 uNgwengwe, *Cynodon dactylon*.
 Stenotaphrum
 glabrum.
 Dactyloctenium
 ægyptiacum.
 umNini, *Rhamnus zeyheri*.
 Erythroxylon pictum.
 Nobibi, *Halleria lucida*.
 umNofunofu, *Cordia caffra*.
 Nondomela, *Halleria lucida*.
 umNonono, *Strychnos henningsii*.
 uNonqamunqamana, *Xanthium*
 spp.
 iNothwane, *Triumfetta*
 rhomboides.
 isiNoza, *Axonopus semialatus*.
 umNqai, *Celastrus peduncularis*.
 iNqala, *Schmidelia africana*.
 umNqandane, *Royena villosa*.
 isiNqane, *R. villosa*.
 um or iNqayi, *Elæodendron*
 æthiopicum.
 E. laurifolium.
 umNqumo, *Olea verrucosa*.
 umNqwabe, *Erythrina tomentosa*.
 iNqwelambila, *Electronia mundii*.
 iNtsindi, *Randia rudis*.
 isiNuasi, *Vitis capensis*.
 umNuka, *Cassipourea verticillata*.
 umNukambhiba, *Clausena*
 inaequalis.
 uNukane, *Ocotea bullata*.
 variety of *Amabele*.
 umNungumabele, *Xanthoxylon*
 capense.
 umNungwane, *X. capense*.
 isiNwazi, *Vitis cuneifolia*.
 isiNwazana, *Vitis* spp.
 umNweba, *Mimusops caffra*.
 Sideroxylon inerme.
 u(lu)Nwele, *Sutherlandia*
 frutescens.
 Cliffortia sp.
 umNyamathi, *Ekebergia meyeri*.
 E. capensis.
 iNyathelo, *Vernonia woodii*.
 V. mespilifolia.
 uNyalothi, *Panicum typhoideum*.
 uNyawothi, *P. typhoideum*.
 nmNyamati, *Ekebergia capensis*.
 umNyankomo, *Eleusine indica*.
 Chloris gayana.
 uNyenye, *Rhamnus prinoides*.
 umNyegane, *Dovyalis rhamnoides*.
 uNyezane, variety of imFe.

- iQonga, *Burchellia capensis*.
 umQongo, *Clerodendron glabrum*.
 umQoqongo, *C. glabrum*.
 uQontsi, *Eriosema salignum*.
 E. cordatum.
 Qovane, *Eragrostis superba*.
 uQukuvama, *Lantana salviæfolia*.
 isiQulaba, *Faurea macnaughtoni*.
 Protea hirta.
 isiQulabahloti, *Myrsine*
 melanophleas.
 umQulzuzane, *Poa binata*.
 umQuma, *Anastrabe integerrima*.
 Olea verrucosa.
 O. woodiana.
 umQumaswele, *O. foveolata*.
 uQume, *Hippobromus alata*.
 uQunga, *Andropogon dregeanus*.
 A. auctus.
 A. nardus.
 iQunga elinameva, *Scolopia*
 zeyheri.
 iQuniza elinameva, *S. zeyheri*.
 uQuquvama, *Lantana salviæfolia*.
 umQuqoba, *Celastrus buxifolius*.
 Scolopia gerrardi.
 inQutu, *Olinia cymosa*.
 iQwaningi, *Capparis corymbifera*.
 umQwaqwana, *Clerodendron*
 glabrum.
 iQweleba *Erythroxylon zuluense*.
 inQwelambilu, *Plectronia mundii*.
 umQwenge, *Panax gerrardi*.
 uQwengu, *Tephrosia macropoda*.
 T. diffusa.
 umRrasharrasha, *Eragrostis*
 aspera.
 umRrepurrepu, *E. curvula*.
 i(li)Rrolo, *Grewia occidentalis*.
 uSahlulamanye, *Pterocelastrus*
 rostratus.
 Sampasu, *Pavetta lanceolata*.
 Sandulane, *Plectronia mundii*.
 umSanga, *Clausena inæqualis*.
 umSasana, *Dichrostachys nutans*.
 umSekelo, *Pyrenacantha*
 scandens.
 Seluma, *Cunonia capensis*.
 uSelwa, *Sphærosicyos sphæricus*.
 Selwayo, *Curtisea faginea*.
 Sendelenja, *Cucumis africana*.
 umSenge, *Cussonia spicata*.
 C. paniculata.
 umSengembusi, *C. umbellifera*.
 umSengumnyane, *Toddalia*
 natalensis.
 amaSetole, *Mimusops obovata*.
 mhllope, *Mimusops* sp.
 uShaqa, *Berkheya* sp.
 umShekisane, *Euclea lanceolata*.
 isiShoba, *Olinia cymosa*.
 iShongwe, *Xysmalobium*
 lapathifolium.
 isiShoshokazana, *Ranunculus*
 pinnatus.
 Shwaqa, *Wahlenbergia*
 undulata.
 umSimbiti, *Milletia caffra*.
 inSimboshane, *Weihea*
 madagascarensis.
 inSinde, *Anthistiria imberbis*.
 inSindeboia, *Trichopteryx*
 simplex.
 uSinga la salukazi, *Dalbergia*
 obovata.
 inSingane, *Ocotea bullata*.
 umSingizane, *Sporobolus indicus*.
 umSinjane, *Tricalysia capensis*.
 T. sonderiana.
 umSintsana, *Erythrina humei*.
 umSintsi, *E. caffra*.
 umSipane, *Cluytia glabrescens*.
 inSipane, *Calpurnia lasiogyne*.
 Calpurnia spp.
 umSityane, *Olea verrucosa*.
 umSobo, *Solanum nigrum*.
 umSokosoko, *Ethulia conyzoides*.
 u(lu)Solo, *Albizzia fastigiata*.

- umSondeza, *Scutia commersoni*.
 umSonti, *Podocarpus latifolius*.
 umSugusi, *Gardenia globosa*.
 umSugusugu, *G. globosa*.
 uSukumbili, *Hypericum*
 ethiopicum.
 umSulusulu, *Euphorbia tirucalli*.
 Euphorbia sp.
 iSumimbuzi, *Chilianthus*
 arborescens.
 iSundu, *Phœnix reclinata*.
 umSunu wembusi, *Tricalysia*
 lanceolata.
 Nuzia
 floribunda.
 uSununundu, *Acalypha*
 peduncularis.
 umSuswane, *Lippia asperifolia*.
 umSwani-wemvubu, variety of
 Amabele.
 umSwi, *Eugenia cordata*.
 umTala, *Erianthus capensis*.
 umTala ga fula, *E. sorghum*.
 umTala m hlope, *E. sorghum*.
 umTambane, *Stephania*
 hernandifolia.
 inTambiso, *Rubia cordifolia*.
 iTambo, *Nuzia floribunda*.
 isiTambo, *Trichocladus crinitus*.
 inTandela, any climbing plant.
 inTana, *Dioscorea malifolia*.
 maTandazana, *Schmidelia*
 monophylla.
 uTangazana, *Cucumis hirsutus*.
 um, u(lu)Tatawe, *Acacia pennata*.
 inTatasana, *Schmidelia*
 monophylla.
 isiTate, *Oxalis* spp.
 umTate (or i), *Pteroxylon utile*.
 Tato, *Faurea macnaughtoni*.
 inTebe, *Richardia africana*.
 inTelegi, *Crassula* spp.
 inTelisi, *Portulacaria afra*.
 isiTelo, fruit, any kind.
- isiTelelo, *Aster erigeroides*.
 umTelelo, *Ochna arborea*.
 iliTembu, *Sparaxis* sp.
 umTenatene, *Royena lucida*.
 iliTenenende, *Cola natalensis*.
 umTensema, *Ochna arborea*.
 umTente, *Imperata arundinacea*.
 umTepa, *Avenastrum turgidulum*.
 i(li)Tete, *Polygala oppositifolia*.
 iThiela, *Cassinia phyllifolia*.
 umuTi, any plant or medicine.
 umTimane, *Eragrostis major*.
 Panicum
 crus-pavonis.
 umTimatane, *Royena lucida*.
 isiTime, *Hippobromus alata*.
 umTintana, *Eugenia* sp.
 umTitimbila, *Senecio juniperinus*.
 inTlashane, *Lichtensteinia*
 pyrethrifolia.
 inTlokoshane, *Rhus lucida*.
 R. puberula.
 R. villosa.
 R. laevigata.
 inTlunganyembe, *Acocanthera*
 spectabilis.
 inTlunu yomntwana, *Vangueria*
 latifolia.
 Tobankone, *Burchellia*
 capensis.
 maTohlwane, *Eragrostis*
 chalcantha.
 umTolo, *Acacia* sp.
 inTolwane, *Elephantorrhiza*
 burchellii.
 umTombe, *Ficus natalensis*.
 umTombo, *Cissampelos torulosa*.
 Polygala myrtifolia.
 isiTomboti, *Acalypha glabrata*.
 umTomboti, *Spirostachys*
 africana.
 Tondo, *Pterocarpus erinaceus*.
 inTondo, *Argyrolobum*
 marginatum.



- Tongoti, *Gardenia neuberia*.
 umTongwane, *Chrysophyllum*
 natalensis.
 C. viridifolium.
 Cryptocarya spp.
 Oncoba spinosa.
 umTonjana, *Ficus* spp.
 umToto, *Odina edulis*.
 umTotovane, *Solanum*
 auriculatum.
 Totshe, *Xymalos monospora*.
 Totshwa, *X. monospora*.
 inTovani, *Rhus gerrardi*.
 inTozane, *Lasiosiphon*
 anthylloides.
 Peddiea africana.
 Dais cotinifolia.
 umTsaba, *Andropogon ruprechtii*.
 inTshakaza, *Osyris abyssinica*.
 inTsangu, *Cannabis sativa*.
 inTsangwana, *Tephrosia*
 kraussiana.
 inTsema, *Euphorbia pugniformis*.
 E. bupleurifolia.
 iTshalo, *Rubus pinnatus*.
 iTshalo elimnyama, *Rubus* sp.
 elibomvu, *Rubus* sp.
 uTshani, grass of any kind.
 uTshetshan, *Chilianthus arboreus*.
 umTshepisana, *Euclea lanceolata*.
 umTshiki, *Eragrostis plana*.
 Tshikisani, *Euclea lanceolata*.
 E. natalensis.
 Tshikivane, *Maba natalensis*.
 isiTshimbe, *Andropogon hirtus*.
 inTshitshi, *Leucosidea sericea*.
 iTshola benyoni, *Alberta magna*.
 umTshongi, *Antidesma venosum*.
 inTshongwana, *Xysmalobium* sp.
 inTshongwe, *Xysmalobium* sp.
 isiTshube, *Andropogon*
 appendiculatus.
 Elionurus argenteus.
 umTshumo, *Arundinella ecklonii*.
 inTshunga, *Momordica fætida*.
 inTshungwana, *M. involucrata*.
 inTshwala benyoni, *Leonotis* spp.
 inTsihlo, *Capparis citrifolia*.
 inTsikane, *Cyperus* spp.
 inTsinde, *Anthistiria imberbis*.
 inTsindwane, *Peliostomum*
 calycinum.
 umTuma, *Solanum sodomæum*.
 S. melongena.
 inTuma, *Solanum* spp.
 isiTumana, *S. capense*.
 inTumbanhlosi, *Croton*
 gratissimum.
 umTumyalele, *Pleurostyli*
 capensis.
 umTunduluka, *Ximenia caffra*.
 inTunga, *Andropogon hirtus*.
 Andropogon spp.
 Tungagazane, *Chrysophyllum*
 natalensis.
 inTungamusi, *Pennisetum*
 cenchroides.
 umTungulu, *Carissa grandiflora*.
 umTungwa(na), *Cryptocarya*
 woodii.
 inTungwane, *Gardenia globosa*.
 isiTupe, *Andropogon contortus*.
 Trachypogon
 polymorphus.
 isiTutshana, *Weihea gerrardi*.
 iTwakele, *Rinorea ardiseæfolia*.
 umTwazi, *Vitis rhomboidea*.
 iTywina, *Pterocelastrus*
 variabilis.
 isiUlulu, *Secamone thunbergii*.
 umVala sangwane, *Gardenia*
 thunbergii.
 umVama, *Celastrus cordatus*.
 umVangazi, *Trema bracteolata*.
 T. orientalis.
 umVelwayo, *Curtisea faginea*.
 uVeti, *Xymalos monospora*.
 uVeto, *X. monospora*.

- ubuVimba, *Withania somnifera*.
 umViti, *Kiggelaria dregeana*.
 Eragrostis plana.
 uViti, *E. curvula*.
 umViyo, *Vangueria infausta*.
 wehlati, *V. lasiantha*.
 totshana, *Vangueria* sp.
 umVuma, *Turraea floribunda*.
 umVumu, *Sapium mannianum*.
 umVumvu, *Celtis kraussiana*.
 C. rhamnifolia.
 uVungu, *Trichilia emetica*.
 umVusamkunzi, *Carissa arduina*.
 umVutwamini, *Plectronia ventosa*.
 P. spinosa.
 umVuzane, *Lasiosiphon kraussii*.
 umWele, *Cliffortia strobilifera*.
 Wezimpisi, *Royena villosa*.
 iWili, *Andropogon sorghum*.
 umXaba, *Dombeya cymosa*.
 umXakanje m'kulu, *Pavetta*
 lanceolata.
 umXaleba, *Cryptocarya* sp.
 Xalote, *Pygeum africanum*.
 uXapozi, *Ranunculus pinnatus*.
 amaXapozi, *Leersia hexandra*.
 Xelegengane, *Gardenia rothmanni*.
 umXenga, *Panax gerrardi*.
 i(li)Xoboxobo, *Osteospermum*
 grandidentatum.
 Xoboti, *Cryptocarya* sp.
 iXolo, *Trichilia emetica*.
 umXopo, *Fuirena pubescens*.
 Xossobe, *Homalium rufescens*.
 umXozane, *Kyllinga elatior*.
 Xulalembile, *Plectronia*
 obovata.
 umYaka, *Chloris gayana*.
 umYakayi, *Mimusops caffra*.
 umYukazane, *Andropogon*
 ceresiæformis.
 i(li)Yala, *Smilax kraussiana*.
 Yali, *S. kraussiana*.
 iYenda, variety of imFe.
 iYoli, *Datura stramonium*.
 Zahlulumanye, *Pterocelastrus*
 variabilis.
 P. rostratus.
 inZala, any kind of grass seed.
 umZane, *Toddalia natalensis*.
 T. lanceolata.
 iZaza, *Smilax kraussiana*.
 iZeli, *Psychotria capensis*.
 Zeti, *Gerrardiana foliosa*.
 umZezana, *Salix capensis*.
 iZibu, *Nymphaea stellata*.
 umZilanyoni, *Croton sylvaticus*.
 uZililo, *Stapelia gigantea*.
 Huernia hystrix.
 umZimane, *Olea laurifolia*.
 isiZimane, *Euclea natalensis*.
 Celastrus procumbens.
 ,, mnyama, *Olea*
 laurifolia.
 ,, mhlope, *O. foveolata*.
 Toddalia
 natalensis.
 i(li)Zimba = imFe.
 umZimbiti, *Milletia caffra*.
 i(li)Zingati, *Curtisea faginea*.
 umZinkawu, *Sapindus*
 oblongifolius.
 umZingulu, *Kigelia pinnata*.
 umZombocani, *Strophanthus*
 natalensis.
 Zongazonga, *Oncinotis inandensis*.
 umZungulu, *Dalbergia obovata*.
 D. armata.

EXPLANATION OF PLATES XXII-XXVI,

Illustrating Prof. J. W. Bews' paper, "The Plant Ecology of the Coast Belt of Natal."

PLATE XXII.

FIG. 1.—Umgababa, May 29th, 1919. Strand vegetation and psammophilous bush. In the foreground *Hydrophylax carnosa* is dominant with a clump of *Gazania uniflora* in the right-hand corner. At the edge of the *Hydrophylax* consociates a few spreading specimens of *Ipomæa biloba* are seen growing over the sand (cf. 'Ann. of Nat. Mus.,' vol. ii, pl. xiv). In the background psammophilous bush with *Mimusops caffra*, dominant; *Osteospermum moniliferum* and *Cynanchum obtusifolium* abundant around the margin.

FIG. 2.—Umgababa, May 29th, 1919. Psammophilous scrub. In the foreground *Scævola lobelia* is dominant nearest the sea. Further up *Osteospermum moniliferum*, *Brachylæna discolor* and *Aloe thraskii*.

PLATE XXIII.

FIG. 1.—Umgababa, May 29th, 1919. Climax sand-dune bush. *Strelitzia augusta*, *Sapium mannianum*, *Harpephyllum caffrum*, *Antidesma venosum*, *Carissa grandiflora*, *Erythrina caffra*, *Grewia occidentalis*, *Psychotria capensis*, *Xanthoxylon capensis*, *Trema bracteolata*, *Mimusops caffra*, *Dalbergia armata*, *Schmidelia erosa*, *Strychnos spinosa*, *Celastrus buxifolius* and numerous other species.

FIG. 2.—Umgababa, May 29th, 1919. Tree veld (cf. text-fig. 3). A clump of trees showing *Strelitzia augusta* to the right and *Cussonia spicata* to the left; *Erythrina caffra* and *Antidesma venosum* in the background.

PLATE XXIV.

FIG. 1.—Verulam, May 11th, 1919. Thorn veld. *Acacia horrida* (young trees) in the foreground. *Acacia horrida*, *A. arabica* var. *kraussiana*, *Dichrostachys nutans*, *Euphorbia* sp. (probably *E. similis*), *Celastrus buxifolius*, *Randia dumetorum*, *Cordia caffra*, *Strychnos gerrardi*, forming thorny scrub in the background.

FIG. 2.—Umgababa, May 29th, 1919. Tree veld. *Eugenia cordata* (umDoni or Waterboom) is shown deformed by the east wind. The fact that it is bent over from near the base shows that this area has been bare and wind-swept for at least as long a period as is represented by the age of the tree, i. e. about fifty years probably. In front and to the left of the *Eugenia* young specimens of *Hyphæne crinita* (Ilala palm) are shown. To the left of the photograph a patch of scrub with *Sapium mannianum* dominant around the margins but with *Strelitzia angusta*, *Albizzia fastigiata*, *Antidesma venosum*, *Schmidelia erosa*, *Sapindus oblongifolius*, *Bridelia micrantha*, *Plectronia ventosa* and *Brachylæna discolor*, all common. This scrub is progressive, as is shown by the dead or dying specimens of the light-demanding *Hyphæne crinita* just within its margin which it has overtaken.

PLATE XXV.

FIG. 1.—Durban Bay, August, 1911. Mangrove associates. *Avicennia officinalis* dominant. Its breathing roots are seen growing up through clumps of *Salicornia* sp. and *Chenolea diffusa*.

FIG. 2.—Umbilo, May 10th, 1919. To the left *Avicennia officinalis* growing in brackish water; to the right *Phragmites communis* in fresh water but giving way to *Hibiscus tiliaceus*, *Eugenia cordata* and *Ficus natalensis*, i. e. to hygrophilous bush in the background.

PLATE XXVI.

FIG. 1.—Stella Bush near Durban, May 10th, 1919. Coast Forest. *Protorhus longifolia*, *Trema bracteolata*, *Vangueria lasiantha* and a variety of other species.

FIG. 2.—The same as Fig. 1 but photographed inside. This photograph, using the same plates, aperture, etc., was given 400 times the exposure of the other. *Psychotria capensis* is abundant in the dense shade. The thick woody liane is *Dalbergia armata* and the more delicate herbaceous climber *Flagellaria guineensis*.



Fig. 1.—Strand Vegetation and Psammophilous Bush near Umgababa.



Fig. 2.—Sand Dune Scrub on the South Coast.



Fig. 1.—Sand Dune Bush.



Fig. 2.—*Strelitzia augusta* and *Cussonia spicata* in Tree Veld.



Fig. 1.—Thorn Veld on the Coast Belt near Verulam.



Fig. 2.—Tree Veld on the South Coast. Ilala Palm (*Hyphæne crinita*) and *Eugenia cordata* deformed by the East Wind.



Fig. 1.—Mangrove Vegetation (*Avicennia officinalis*) on the Durban Flats.

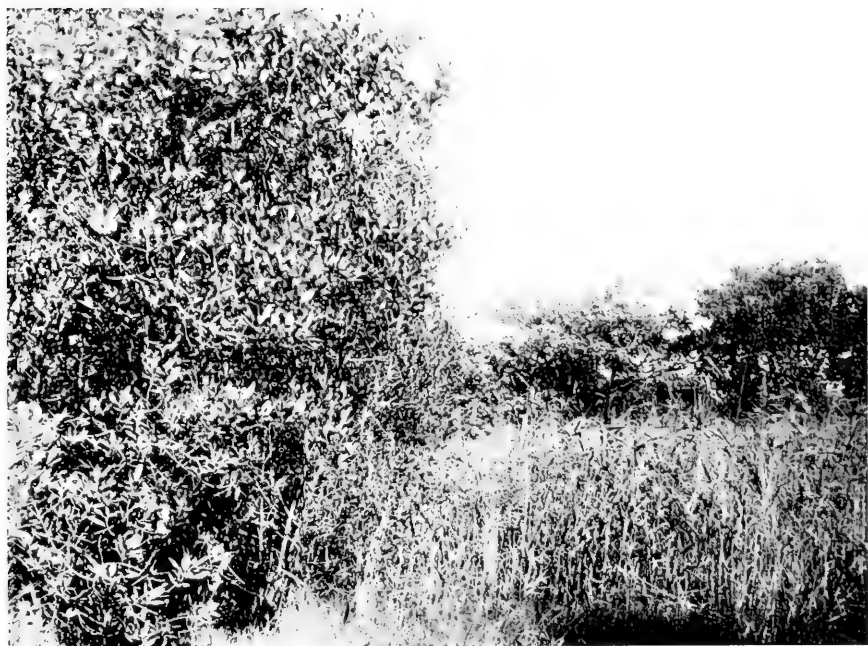


Fig. 2.—Three Stages of Succession: *Avicennia officinalis*, *Phragmites communis*, and *Eugenia cordata*.



Fig. 1.—Coast Forest near Durban.



Fig. 2.—Coast Forest Inside.



Contributions to a Knowledge of the Terrestrial Isopoda of Natal.

Part III.

By

Walter E. Collinge, D.Sc., F.L.S., etc.,

Carnegie Fellow, and Research Fellow of the University of
St. Andrews.

With Plates XXVII-XXXII.

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INTRODUCTION.

THANKS to the untiring labours of Drs. E. Warren and C. Akerman, I am able in the present contribution to add a further series of new Terrestrial Isopoda to the fauna of Natal and the adjacent country.

It is evident from the work that has already been carried out that Natal, indeed the whole of South Africa, possesses a rich Isopodean fauna, and of the specimens collected there yet remain a number of new forms, but the material at present in my hands is insufficient for description.

In the present paper figures of all the new species are given, including those described in Part I (3), and I have to thank Miss Grace Edwards and Miss E. R. Burnett for the care they have expended upon these.

The new forms include a species of *Ligia Fabr.*, one belonging to the genus *Alloniscus Dana*, four new species of *Cubaris Brandt*, and one of the new genus *Anchicubaris*. In addition to these I am able to record the occurrence of *Philoscia muscorum (Scopoli)* and *Porcellionides pruinosus (Brandt)*, and some further localities for *Philoscia warreni Collge.* and *P. dilectum Collge.*

I. DESCRIPTION OF GENERA AND SPECIES.

LIGIA Fabricius.

Comparatively little has been written upon the members of this interesting genus. Structurally they are easily distinguished by well-defined characters and many of the species are exceedingly common and have a wide distribution.

Hitherto the genus has not been recorded from Natal, although it has long been known from Cape Colony. Brandt (1) in 1833 described very briefly the *Ligia glabrata* and *L. dilatata*, and Budde-Lund (2) in 1885 described in the briefest possible manner the *L. gracilipes*.

So far as I am aware none of these have been adequately described or figured.

For the specimens of *L. dilatata* I am indebted to the kindness of Mr. Keppel H. Barnard, of the South African Museum; the rest of the material has been obtained by Dr. Conrad Akerman.

Brandt's descriptions are very short, and as his work is not readily accessible I repeat them here :

a. Corpore oblongo.

Ligia glabrata n. sp. Antennarum articuli apicales margine superiore ciliati. Appendicum caudalium articulus basalis tetragono-oblongus, haud impressus.

Patria : Caput bonæ spei.

β. Corpore ovato.

Ligia dilatata n. sp. Appendicum caudalium articulus basalis mediocris, tetragono-oblongus.

Patria : Caput bonæ spei.

Krauss (4) gives the size of *L. glabrata* as 11 lines in length and 5·5 in breadth.

In 1885 Budde-Lund re-described both species; but his material seems to have been poor. He further very briefly described a new species under the name of *Ligia gracilipes*, from a few specimens in the Simon Museum, obtained at Laudana.

The question naturally arises, "Are these three referable to one species or are they distinct from one another?" The material I have examined helps us to answer partly this question.

There is no doubt as to Brandt's *L. dilatata*. His *L. glabrata*, I am inclined to think, is only an immature form of the former, whilst Budde-Lund's *gracilipes* is insufficiently described to pronounce an opinion on. The only two statements of any value which this author gives are that the flagellum of the antenna contains 22 joints and that the animal is from 7–9 mm. long. Possibly *gracilipes* is only a young form of some species. In comparing it with specimens

of *L. natalensis* of 7-9 mm. in length I note that this latter species has only 12-15 joints in the flagellum.

In young *L. oceanica* (*Linn.*) of from 7-9 mm. in length both the antennæ and uropoda are proportionally shorter than in the adult and there are always fewer joints in the flagellum of the antennæ.

The original description of *gracilipes* is as follows:

"Speciesi præcedenti affinis, forma et habitu simillima.

"Antennæ exteriores gracillimæ, corpus longitudine quarta parti superantes. Flagellum 22-articulatum; articuli longiores.

"Pedes caudales anales perlongi, corpore paulo longiores.

"Long. 7-9 mm.

"Patria: Africa meridionalis; e 'Laudana' exempla pauca in Museo Simon asservantur."

1. *Ligia natalensis* *n. sp.* Pl. XXVIII, figs. 9-18.

Body (fig. 9) elongated, more than twice as long as it is broad, moderately convex and slightly granulated; metasome abruptly contracted. Cephalon (figs. 10, 11) semi-oval from above with posterior transverse groove; epistome with three prominent transverse ridges, the ventral one with two small upwardly directed spines. Eyes large and convex. Antennulæ (fig. 12) small, first two joints subequal, third joint nodiform. Antennæ (fig. 13) slender and elongated, first three joints small, 4th and 5th elongated, flagellum consisting of 21 joints and short terminal style. First maxilla (fig. 14) small, outer lobe with six stout, elongated, pointed spines and four inner ones varyingly denticulate, inner lobe with three elongated, setose, terminal spines, and prominent setaceous knob. Segments of the mesosome sub-equal, 1st to 3rd with pleural plates truncate terminally, 4th somewhat similar, but with posterior angles pointed, terminal portion of 5th to 7th curved backward and terminating in sharp point. Appendages (figs. 15 and 16) comparatively small and fragile, gradually enlarging from before backwards. Uropoda (fig. 17) elongated and slightly curved

inwards, basal joint wider proximally than distally, endopodite slightly curved and usually shorter than the exopodite and with much longer terminal style; both one and a-half times longer than the basal joint, setaceous. Telson (fig. 18) fairly long, anterior margin prominent and rounded laterally, posterior margin spinous.

Length 16–17 mm.

Colour (in alcohol) silver-grey, with darker greyish markings.

Habitat.—Umlhali, May, 1916. Winkle Spruit Beach, South Coast, Dec. 1916 (C. Akerman).

Type.—In the Natal Museum.

2. *Ligia dilatata* Brandt. Pl. XXVIII, figs. 19–27.

Ligia dilatata Brandt, Bull. Soc. Imp. Nat. Moscou, 1833, vol. vi.

? *Ligia glabrata* Brandt, *ibid.*, p. 172.

Lygia dilatata Krauss, Südafrik. Crust., 1843, p. 62.

Ligia dilatata White, List Crust. Brit. Mus., 1847, p. 98; Budde-Lund, Crust. Isop. Terr., 1885, p. 262.

? *Ligia gracilipes* Budde-Lund, *ibid.*, p. 270.

Ligia dilatata Stebbing, Ann. South Afr. Mus., 1910, vi, p. 437.

Body (fig. 19) oval or oblong oval, slightly convex dorsally and finely granulated; metasome not abruptly contracted. Cephalon (fig. 20) semi-oval from above, with posterior transverse groove; epistome with three transverse ridges. Eyes large and convex. Antennulæ (fig. 21) small, 3-jointed, terminal joint rudimentary. Antennæ (fig. 22) robust and elongated; flagellum with 15 joints. First maxilla (fig. 23), outer lobe with five stout, pointed spines and five inner ones varyingly denticulate; inner lobe with three setose terminal spines, the first of which has a prominent knob. Mesosome with the pleural plates greatly expanded; the 1st partly flanks the cephalon, 2nd to 4th truncate terminally, 5th to 7th with their posterior angles directed backward. Pleural plates of metasome also expanded. First mesosomatic appendage (fig. 24) with all the joints deeply

grooved and the carpopodite globose. Uropoda (fig. 26) comparatively small, basal joint slightly curved towards the inside, endopodite straight and rather longer and wider than the straight exopodite, both with terminal styles. Telson (fig. 27) rather short, anterior margin prominent and rounded.

Length 31 mm.

Colour (in alcohol) light brownish-grey, with darker greyish markings.

Habitat.—Cape Peninsula (K. H. Barnard).

ALLONISCUS *Dana*.

This genus was founded by Dana in 1854. Some two dozen species have been described as belonging to this genus, but it is doubtful whether they are all correctly assigned. It has a wide distribution, having been recorded from North and South America, South Africa, Madagascar, India, Siam, and numerous Pacific islands.

3. *Alloniscus marinus* *n. sp.* Pl. XXIX, figs. 28–38.

Body (fig. 28) oblong oval, strongly convex, finely tuberculated. Cephalon (figs. 29 and 30) convex above, with well-defined frontal margin, which is produced in the median line, cephalic lobes absent, epistome slightly concave with well-marked transverse ridge above the antennal sockets. Eyes oval, fairly large. Antennulæ (fig. 31) short and stout, 3-jointed, terminal joint with lateral setæ and two enlarged setæ at the distal extremity. Antennæ (figs. 32 and 33) of medium length, joints 1–3 small, 4th joint longer and stouter, 5th joint elongated and narrow; flagellum 3-jointed, proximal joint the longest, remainder almost subequal, terminal style short. First maxilla (fig. 34) with outer lobe terminating in nine stout, bluntly ending spines, strong setæ on the outer side; inner lobe wide, with two short setose spines, the inner one being slightly lower in position than the outer one.

Maxillipeds (fig. 35) with wide lobes, outer lobe with few setæ on the end of the 3rd joint and two setose papillæ on the 2nd joint, 1st joint narrow with two large spines; inner lobe with setaceous pad terminally and circle of fine setæ below. The segments of the mesosome are almost subequal excepting the 1st, the pleural plates of which are expanded and flank the cephalon; the remainder are flattened, with the terminal margin truncate, 4-7 with the posterior angle slightly produced backward. The metasome is comparatively small, the two first and part of the 3rd segment being covered by the last mesosomatic segment. Uropoda (figs. 36 and 37) with stout basipodite, thinner on the inner margin, exopodite short and conical, endopodite slightly shorter and more slender, both setaceous and with fine terminal styles. Telson (fig. 38) triangular, apex rounded.

Length 12 mm.

Colour (in alcohol) yellow with brownish mottling, forming a broken median longitudinal line. Posteriorly on each segment of the mesosome and above the pleural plate is an almost circular black spot.

Habitat.—Winkle Spruit Beach, S. Coast, Natal, Dec. 1916 (C. Akerman). Salisbury Island, shore, in sand, uncommon, Aug. 7th, 1916 (Bell-Marley).

Type.—In the Natal Museum.

This is a handsome and conspicuous species, and according to Dr. Akerman common in the sand at the junction of vegetation and the beach.

The lateral, brownish-black eye-like spots are faintly discernible on the tiny white young taken from the brood-pouch of the female.

PHILOSCIA Latreille.

4. *Philoscia warreni* *Cllege*. Pl. XXVII, fig. 7.

Philoscia warreni *Cllege*, Ann. Natal. Mus., 1917, vol. iii, p. 578.

This interesting species seems to be widely distributed. The following are additional records:

Krantzkop, Natal, Jan. 1915 (E. Warren). Isipingo, Natal, Sept. 1915 (C. Akerman). Pietermaritzburg, Jan. 1916 (C. Akerman). Newlands, Cape Town, Jan. 1916 (E. Warren). Sarnia, nr. Durban, 1916 (Mrs. Warren). Buffalo River, East London, Cape Province, Jan. 1916 (E. Warren). Thornybush, Durban Road, eight miles from Pietermaritzburg, April, 1916 (C. Akerman). Knoll Bush, Hilton Road, April, 1916 (C. Akerman), May, 1916 (E. Warren). Otto's Bluff, nr. Pietermaritzburg, June, 1916 (C. Akerman). Durban, Aug. 1916 (C. Akerman). Bayne's Drift, Nov. 1916 (C. Akerman). Mt. Fongosi, Zululand, Jan. 1917 (W. E. Jones). Ntimbankulu, Mid-Illovo, Oct. 1917 (H. C. Burnup). Umhlali, Natal (C. Akerman).

5. *Philoscia dilectum* *Collge.* Pl. XXVII, fig. 8.

Philoscia dilectum *Collge.*, Ann. Natal Mus., 1917, vol. iii, p. 579.

The following are additional records for this species :

Krantzkop, Natal, Jan. 1915 (E. Warren). Sweetwaters Bush, Pietermaritzburg, Aug. 1915 (E. Warren). Isipingo, Natal, Sept. 1915 (C. Akerman). Pietermaritzburg, Jan. 1916 (C. Akerman). Thornybush, Pietermaritzburg, Feb. 1916 (C. Akerman). Sarnia, nr. Durban, 1916 (Mrs. Warren). Buffalo River, East London, Cape Province, Jan. 1916 (E. Warren). Otto's Bluff, nr. Pietermaritzburg, June, 1916 (C. Akerman). Durban, Aug. 1916 (C. Akerman). Bayne's Drift, Nov. 1916 (C. Akerman). Botanical Garden (wild portion), Pietermaritzburg, Dec. 1916 (E. Warren). Mt. Fongosi, Zululand, Jan. 1917 (W. E. Jones). Ntimbankulu, Mid-Illovo, Oct. 1917 (H. C. Burnup). Umhlali, Natal (C. Akerman).

6. *Philoscia muscorum* (*Scopoli*).

Oniscus muscorum, *Scopoli*, Entomol. Carnio., 1763, p. 415.

Habitat.—Knoll Bush, Hilton Road, Aug., 1916 (C. Akerman). Ntimbankulu, Mid-Illovo, Oct. 1917 (H. C. Burnup).

A single specimen from the former locality and two from the latter.

PORCELLIONIDES *Miers* = METAPONORTHUS *Budde-Lund*.

7. *Porcellionides pruinus* (*Brandt*). Pl. XXIX,
figs. 39-47.

Porcellio pruinus *Brandt*, Bull. Soc. Nat. Moscow, 1833, vi, p. 181.

Although there are many slight differences in these specimens from the typical *P. pruinus*, they are not, in my opinion, sufficient to separate them as a distinct species; it is possible, however, that further material may show greater differences. The structural features shown on Pl. XXIX are of specimens collected by Dr. Akerman at Pietermaritzburg, Feb., 1916.

Habitat.—Museum Garden, Pietermaritzburg, Sept. 1915 (E. Warren). Pietermaritzburg, Feb. 1916 (C. Akerman). Durban, Aug. 1916 (C. Akerman).

These specimens differ from British examples of this species in the following characters:

The frontal margin of the cephalon is obtusely pointed in the median line (fig. 39) and not nearly straight as in the typical form. In the antennæ the two joints of the flagellum are almost equal in length, the proximal one being only a little larger than the distal one (fig. 41). The outer lobe of the 1st maxilla (fig. 42) has the six inner spines sharply denticulated, or perhaps it would be more correct to describe them as having bifid terminations. The inner lobe distally is truncate. The second maxilla is comparatively wider and more robust and the same remark applies to the maxillipede (fig. 44). The appendages of the metasome are also slightly more robust. The telson is somewhat elongated, extending beyond the basal plates of the uropoda, and there are minor differences in the various parts of these latter appendages (Figs. 46 and 47).

*CUBARIS Brandt.*8. *Cubaris truncatus* *n. sp.* Pl. XXX, figs. 48-56.

Body (fig. 48) oblong-oval, convex, surface finely granulose. Cephalon (figs. 49, 50) small, flanked by the pleural plates of the 1st mesosomatic segment, anterior margin raised, cephalic lobes absent; epistome slightly convex. Eyes fairly large, situated dorso-laterally. Antennæ (fig. 51) short; flagellum 2-jointed, distal joint rather more than twice the length of the proximal one, terminal style small and conical. First maxillæ (fig. 52), outer lobe terminating in four stout curved spines and six smaller pointed ones; inner lobe slightly grooved on its inner side with two setose spines. Maxillipedes (fig. 53): the terminal joint of the outer lobe is multispinous; there are two spines on the middle joint, and two on the inner side of the basal joint; the inner lobe has a tooth-like spine and a single plain spine. The segments of the mesosome have the pleural plates well developed; those of segments 2-4 are rounded terminally and those of 6 and 7 truncate; posterior angles not produced. Uropoda (fig. 55) not extending beyond the telson, basal plate short, wide, and thick, slightly raised and convex on the posterior outer margins, posterior margin truncate, antero-dorsal surface expanded and thickened; exopodite short, not extending to the posterior margin of the basal plate; endopodite longer and broader, slightly keeled, setaceous. Telson (fig. 56) not extending beyond the uropoda, width greater than the length, lateral margins very slightly curved, expanded anteriorly and slightly keeled, posterior margin truncate.

Length 12.5 mm.

Colour (in alcohol) yellowish-brown with darker brown mid-dorsally and laterally, flecked with yellow.

Habitat.—Pt. Alfred, Cape Province (J. Hewitt).

Type.—In the Albany Museum.

9. *Cubaris akermani* n. sp. Pl. XXX, figs. 57-66.

Body (fig. 57) oblong-oval, convex, surface very finely granulose. Cephalon (figs. 58 and 59) small, flanked by the pleural plates of the 1st mesosomatic segment; anterior margin raised, cephalic lobes absent; epistome dorsally sloping, slightly concave laterally and raised in the median line. Eyes large, situated dorso-laterally. Antennæ (fig. 60) short and slender, setaceous and grooved on the outer side of each peduncular joint; flagellum 2-jointed, distal joint three times as long as the proximal one, elongated terminal style. First maxillæ (fig. 61), outer lobe terminating in five stout curved spines and six smaller ones; inner lobe slightly grooved on the inner side and bluntly pointed terminally, with two setose spines. Maxillipedes (fig. 62), the terminal joint of the outer lobe is multispinous, and there are seven spines on the middle joint; the inner lobe is broad and has four spines, one arising from a central papilla-like portion. The segments of the mesosome have the pleural plates of 2-4 rounded terminally, 5-7 truncate, posterior angles not produced. The coxopodite on the inner margin of the underside of the 1st segment is well-developed (fig. 63) and there is a definite groove on both segments 1 and 2. Uropoda (figs. 64 and 65) not extending beyond the telson, basal plate short and wide, slightly raised and convex on the posterior and outer margins, posterior margin wide and truncate, antero-dorsal surface expanded; exopodite short with terminal style, not extending to the posterior margin of the basal plate; endopodite much longer and widest at its proximal end, setaceous. Telson (fig. 66) not extending beyond the uropoda, width greater than the length, lateral margins curved, expanded anteriorly, with single median raised notch on anterior margin, posterior margin very faintly curved.

Length 23 mm.

Colour (in alcohol) almost black dorsally with very faint greyish flecks laterally.

Habitat.—Sweetwaters Bush, Pietermaritzburg, July, 1916 (E. Warren). Mt. Fongosi, Zululand, Feb. 1917 (W. E. Jones).

Type.—In the Natal Museum.

Externally this species bears a superficial resemblance to *C. burnupi*, *Collge.*, but it is larger and rather more convex anteriorly.

10. *Cubaris barnardi* n. sp. Pl. XXXI, figs. 67-76.

Body (fig. 67) oblong-oval, moderately convex, surface very finely granulose, excepting for a series of lateral patches, each with four raised flecks on each side of the median line. Cephalon (figs. 68, 69) small, covered with minute spines, flanked by the pleural plates of the 1st mesosomatic segment, anterior margin raised; epistome with upper portion spinous below and laterally smooth and almost flat. Eyes fairly large and raised from the cephalon, situated dorso-laterally. Antennulæ (fig. 70) short, 3-jointed, with few lateral setæ on the distal joint. Antennæ (fig. 71) with the 4th and 5th joints elongated; flagellum 2-jointed, the proximal joint being the smaller. First maxilla (fig. 72) small, outer lobe with four stout curved spines and six smaller ones, setose on the outer margin and slightly expanded at the distal end; inner lobe with three setose spines. The segments of the mesosome have the pleural plates well developed; 1st segment with the posterior angle slightly notched (fig. 73); terminal margin of remainder truncate, all with slightly raised median ridge and directed backwardly. The pleural plates of the metasome somewhat elongated. Uropoda (fig. 75) small, not extending beyond the telson, basal plate short and narrow, considerably raised and convex, posterior margin pointed, antero-dorsal surface expanded; exopodite extending almost to the posterior margin of the basal plate, endopodite longer and more robust, both setaceous. Telson (fig. 76) extending very slightly beyond the uropoda, length greater than the width, lateral margins almost straight, expanded anteriorly, posterior margin very faintly curved.

Length 20·5 mm.

Colour (in alcohol) dark grey with lighter grey mottling in the median and lateral areas.

Habitat.—Sarnia nr. Durban, Oct. 1916 (E. Warren). Winkle Spruit Beach, S. Coast, Dec. 1916 (C. Akerman). Mt. Fongosi, Zululand, Jan. 1917 (W. E. Jones).

Type.—In the Natal Museum.

11. *Cubaris griseus* n. sp. Pl. XXXI, figs. 77–85.

Body (fig. 77) oblong-oval, strongly convex and finely rugose. Cephalon (figs. 78, 79) small and flanked by the pleural plates of the 1st mesosomatic segment, slightly raised in the mid-dorsal line and faintly marked with light-coloured, irregularly shaped rugosities; anterior margin raised and turned slightly backward; epistome smooth and convex. Eyes prominent, situated dorso-laterally. Antennulæ small 3-jointed. Antennæ (fig. 80) with the 5th joint elongated; flagellum 2-jointed, the proximal joint less than one-third the length of the distal joint, terminal style short (fig. 81). First maxillæ (fig. 82) small, outer lobe with four short curved spines and six smaller and more slender ones, setose on the outer margin; inner lobe fairly wide with two small setose spines arising from the inner distal margin. Segments of the mesosome strongly convex, the 1st with expanded pleural plates, with margins slightly reflected upwards and outwards, anterior angle acutely pointed, posterior angle less so, pleural plates of 2nd to 4th segments slightly excavate, remainder truncate, posterior angles only very slightly produced. Notch and groove on the under side of the inner margin of segments 1 and 2 well-developed (fig. 83). Uropoda (fig. 84) robust, not extending beyond the telson, basal plate thick, strongly raised and convex dorso-laterally, posterior margin truncate, antero-dorsal surface folded, expanded slightly below the point of articulation of the endopodite, setaceous; exopodite short and stout, not extending to the posterior margin of the basal

plate, setaceous, endopodite long and stoutly built, somewhat flattened and setaceous. Telson (fig. 85) with posterior margin wider than the length, almost truncate, lateral margins slightly curved inward, expanded anteriorly, with raised triangular area in the centre.

Length 8 mm.

Colour (in alcohol) a pearly-grey, with very faint lighter-coloured flecks.

Habitat.—Knöll Bush, Hilton Road, Aug. 31st, 1916 (C. Akerman).

Type.—In the Natal Museum.

ANCHICUBARIS gen. nov.

Body oblong-oval, strongly convex, with thickened lateral ridges on the pleural plates, which latter are strongly curved backwardly and outwardly, terminally truncate, dorsally produced upwardly and outwardly. Cephalon with greatly produced and flattened epistome. Antennulæ absent. Telson extending slightly beyond the uropoda. Remaining characters as in *Cubaris*.

I have thought it advisable to separate the specimens from Mt. Fongosi, etc., from the genus *Cubaris* on account of the form of the pleural plates of the mesosome and the greatly produced anterior margin of the cephalon.

12. *Anchicubaris fongosiensis n. sp.* Pl. XXXII, figs. 86-96.

Body (fig. 86) oblong-oval, strongly convex, dorsal surface with prominent tubercles. Cephalon (figs. 87, 88) small and tuberculated, with two anterior eminences; the anterior margin is greatly produced as a flattened plate, flanked by the pleural plates of the first mesosomatic segment, epistome large and almost flat. Eyes small, situated dorso-laterally. Antennulæ absent. Antennæ (fig. 89) short and robust, setaceous, 2nd and 5th joints slightly grooved on their outer

side; flagellum 2-jointed, the distal joint being two and a half times the length of the proximal one; style elongated with few terminal setæ (fig. 90). First maxillæ (fig. 91) with outer lobe terminating in four stout curved spines and six smaller pointed ones, inner lobe with two short setose spines on the inner margin. The segments of the mesosome (fig. 93) are strongly convex; pleural plates thickened with lateral ridges, strongly curved backwardly and outwardly, terminally truncate, dorsally produced upwardly and outwardly. Each segment has two transverse rows of large tubercles, excepting the 1st, which has four rows. Last three segments of the metasome with broad pleural plates, dorsum of last segment with only two tubercles, remainder with four. Thoracic appendages comparatively small. Uropod (figs. 94, 95) not extending beyond the telson, basal plate thick, strongly raised and convex, posterior margin truncate, antero-dorsal surface broad and convex, dorsally and ventrally with small triangular spines; exopodite short, endopodite longer and more massive, setaceous. Telson (fig. 96) wider than long, extending slightly beyond the uropoda, lateral margins curved inwards, with two prominent tubercles anteriorly, terminal margin truncate or nearly so.

Length 9.5 mm.

Colour (in alcohol) faint yellow with brownish mottling or wholly creamy-white.

Habitat.—Mt. Fongosi, Zululand, July, 1917 (W. E. Jones), Sarnia, nr. Durban, Oct. 1916 (E. Warren), Winkle Spruit Beach, S. Coast, Dec. 1916 (C. Akerman).

Type.—In the Natal Museum.

II. BIBLIOGRAPHY.

1. BRANDT, J. F.—“*Conspectus monographiæ Crustaceorum Oniscodorum Latreillii*,” ‘Bull. Soc. Imp. Nat. Moscou,’ 1883, vol. vi, pp. 171–193.
2. BUDDE-LUND, G.—“*Crustacea Isopoda Terrestria*,” ‘*Hauniæ*,’ 1885, pp. 1–320.

3. COLLINGE, WALTER E.—“Contributions to a Knowledge of the Terrestrial Isopoda of Natal,” Part I, ‘Ann. Natal Mus.,’ 1917, vol. iii, pls. 567–585, pp. xl–xlii.
 4. KRAUSS, F.—‘Die südafrikanischen Crustaceen,’ Stuttgart, 1843.
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EXPLANATION OF PLATES XXVII–XXXII,

Illustrating Dr. Walter E. Collinge’s paper, “Contributions to a Knowledge of the Terrestrial Isopoda of Natal,” Part III.

PLATE XXVII.

- FIG. 1.—× 6. *Cubaris warreni* Collge.
 FIG. 2.—× 8. „ *reticulatus* Collge.
 FIG. 3.—× 3. „ *burnupi* Collge.
 FIG. 4.—× 6·7. „ *natalensis* Collge.
 FIG. 5.—× 6. „ *longicauda* Collge.
 FIG. 6.—× 5. „ *trilobata* Collge.
 FIG. 7.—× 6. *Philoscia warreni* Collge.
 FIG. 8.—× 7. „ *dilectum* Collge.

PLATE XXVIII.

1. *Ligia natalensis* n. sp.

- FIG. 9.—× 6. Dorsal view.
 FIG. 10.—× 10. Dorsal view of the cephalon.
 FIG. 11.—× 10. Anterior view of the cephalon.
 FIG. 12.—× 70. Left antennule, ventral view.
 FIG. 13.—× 10. Right antenna, dorsal view.
 FIG. 14.—× 215. Terminal portion of the inner and outer lobes of the 1st maxilla, ventral view.
 FIG. 15.—× 18. Second mesosomatic appendage.
 FIG. 16.—× 18. Seventh mesosomatic appendage.
 FIG. 17.—× 12. Dorsal view of the left uropod.
 FIG. 18.—× 8. Dorsal view of the telson.

*Ligia dilatata Brandt.*FIG. 19.— $\times 3$. Dorsal view.FIG. 20.— $\times 5.5$. Anterior view of the cephalon.

FIG. 21.—Right antennule, ventral view.

FIG. 22.— $\times 5$. Left antenna, dorsal view.

FIG. 23.—Terminal portion of the inner and outer lobes of the right 1st maxilla, ventral view.

FIG. 24.— $\times 9$. Second mesosomatic appendage.FIG. 25.— $\times 9$. Seventh mesosomatic appendage.FIG. 26.— $\times 6$. Dorsal view of the right uropod.FIG. 27.— $\times 4$. Dorsal view of the telson.

PLATE XXIX.

*Alloniscus marinus n. sp.*FIG. 28.— $\times 5$. Dorsal view.FIG. 29.— $\times 8.5$. Dorsal view of the cephalon.FIG. 30.— $\times 8$. Anterior view of the cephalon.FIG. 31.— $\times 70$. Left antennule, ventral view.FIG. 32.— $\times 24$. Right antenna, dorsal view.FIG. 33.— $\times 220$. Terminal style of antenna.FIG. 34.— $\times 150$. Terminal portion of the inner and outer lobes of the right 1st maxilla, ventral view.FIG. 35.— $\times 82$. Terminal portion of the left maxillipede.FIG. 36.— $\times 21$. Dorsal view of the right uropod.FIG. 37.— $\times 21$. Ventral view of the right uropod.

FIG. 38.—Dorsal view of the telson and last metasomatic segment.

Porcellionides pruinosis (Br.).

FIG. 39.—Dorsal view of the cephalon.

FIG. 40.—Anterior view of the cephalon.

FIG. 41.—Left antenna, dorsal view.

FIG. 42.—Terminal portion of the inner and outer lobes of the right 1st maxilla, ventral view.

FIG. 43.—Second maxilla of right side, ventral view.

FIG. 44.—Terminal portion of the right maxillipede.

FIG. 45.—Second mesosomatic appendage.

FIG. 46.—Dorsal view of the right uropod.

FIG. 47.—Dorsal view of the telson and last metasomatic segment.

PLATE XXX.

Cubaris truncatus n. sp.

- FIG. 48.—× 5. Dorsal view.
FIG. 49.—× 8. Dorsal view of the cephalon.
FIG. 50.—× 8. Anterior view of the cephalon.
FIG. 51.—× 30. Left antenna, dorsal view.
FIG. 52.—× 90. Terminal portion of the inner and outer lobes of the right 1st maxilla, ventral view.
FIG. 53.—× 70. Terminal portion of the right maxillipede.
FIG. 54.—× 8. Underside of the lateral margin of the 1st and 2nd mesosomatic segments.
FIG. 55.—× 28. Dorsal view of the right uropod.
FIG. 56.—× 10. Dorsal view of the telson, uropoda, and last metasomatic segment.

Cubaris akermani n. sp.

- FIG. 57.—× 3. Dorsal view.
FIG. 58.—× 4. Dorsal view of the cephalon.
FIG. 59.—× 4. Anterior view of the cephalon.
FIG. 60.—× 15. Left antenna, dorsal view.
FIG. 61.—× 112. Terminal portion of the inner and outer lobes of the right 1st maxilla, ventral view.
FIG. 62.—× 70. Terminal portion of the right maxillipede.
FIG. 63.—× 6. Underside of the lateral margin of the 1st and 2nd mesosomatic segments.
FIG. 64.—× 18. Dorsal view of the right uropod.
FIG. 65.—× 18. Ventral view of the right uropod.
FIG. 66.—× 7. Dorsal view of the telson, uropoda, and last metasomatic segment.

PLATE XXXI.

Cubaris barnardi n. sp.

- FIG. 67.—× 14. Dorsal view.
FIG. 68.—× 19. Dorsal view of the cephalon.
FIG. 69.—× 19. Anterior view of the cephalon.

FIG. 70.— $\times 150$. Left antennule, ventral view.

FIG. 71.— $\times 30$. Left antenna, dorsal view.

FIG. 72.— $\times 75$. Terminal portion of the inner and outer lobes of the left 1st maxilla, ventral view.

FIG. 73.— $\times 16$. Lateral view of pleural plate of 1st mesosomatic segment.

FIG. 74.— $\times 16$. Underside of the lateral margin of the 1st and 2nd mesosomatic segments.

FIG. 75.— $\times 50$. Dorsal view of the right uropod.

FIG. 76.— $\times 20$. Dorsal view of the telson, uropoda, and last metasomatic segment.

Cubaris griseus n. sp.

FIG. 77.— $\times 8$. Dorsal view.

FIG. 78.— $\times 12.5$. Dorsal view of the cephalon.

FIG. 79.— $\times 12.5$. Anterior view of the cephalon.

FIG. 80.— $\times 28$. Right antenna, dorsal view.

FIG. 81.— $\times 320$. Terminal style of antenna.

FIG. 82.— $\times 115$. Terminal portion of the inner and outer lobe of the left 1st maxilla, ventral view.

FIG. 83.— $\times 28$. Underside of the lateral margin of the 1st and 2nd mesosomatic segments.

FIG. 84.— $\times 50$. Dorsal view of the right uropod.

FIG. 85.— $\times 15$. Dorsal view of the telson and last metasomatic segment.

PLATE XXXII.

Anchicubaris fongosiensis gen. et sp. nov.

FIG. 86.— $\times 9$. Dorsal view.

FIG. 87.— $\times 15$. Dorsal view of the cephalon.

FIG. 88.— $\times 15$. Anterior view of the cephalon.

FIG. 89.— $\times 7.5$. Left antenna, dorsal view.

FIG. 90.— $\times 320$. Terminal style of antenna.

FIG. 91.— $\times 215$. Terminal portion of the inner and outer lobes of the left 1st maxilla, ventral view.

FIG. 92.— $\times 50$. Underside of the lateral margin of the 1st and 2nd mesosomatic segments.

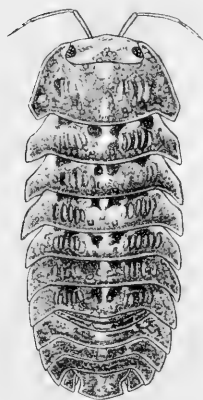
FIG. 93.—Lateral view of the mesosomatic segments showing the peculiar pleural plates.

FIG. 94.— $\times 50$. Dorsal view of the left uropod.

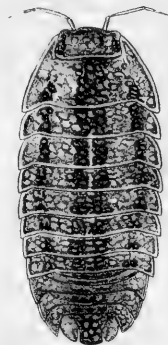
FIG. 95.— $\times 50$. Ventral view of the left uropod.

FIG. 96.— $\times 15$. Dorsal view of the telson and last metasomatic segment.

The author desires to thank the Carnegie Trust for the Universities of Scotland for a grant to defray artists' charges.



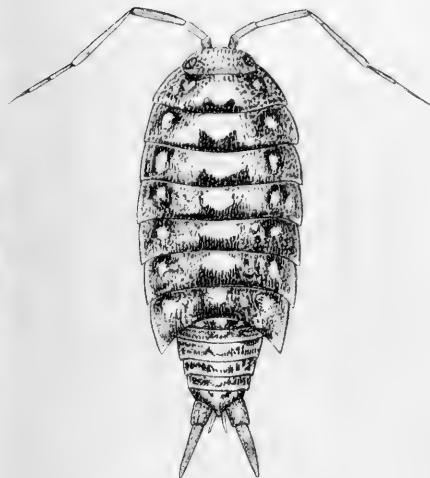
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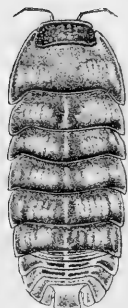
2 x 3



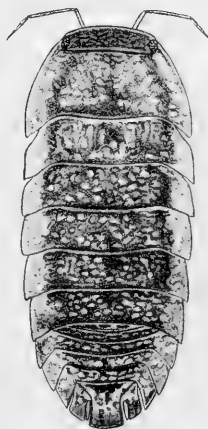
3 x 3



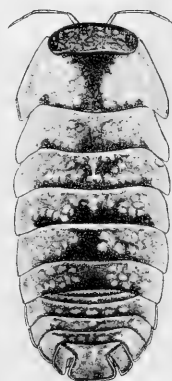
7 x 6.



4 x 6.7.



5 x 6.



6 x 5.



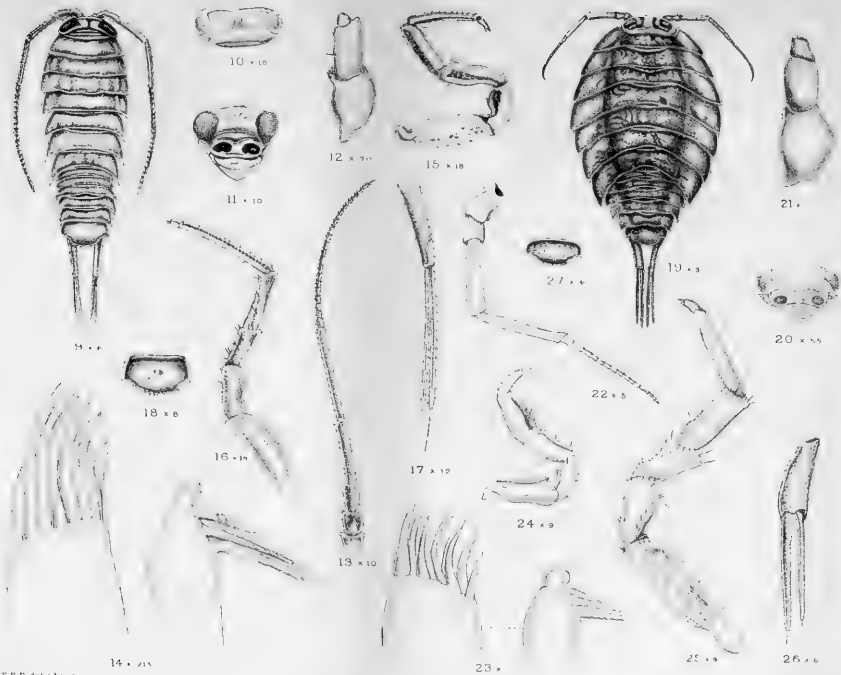
8 x 9.

G.E. del. ad nat.

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CUBARIS WARRENI Clige. fig.1, C. RETICULATUS Clige. fig.2, C. BURNUPI Clige. fig.3,
C. NATALENSIS Clige. fig.4, C. LONGICAUDA Clige. fig.5, C. TRILOBATA Clige. fig.6,
PHILOSCIA WARRENI Clige. fig.7, P. DILECTUM Clige. fig.8.





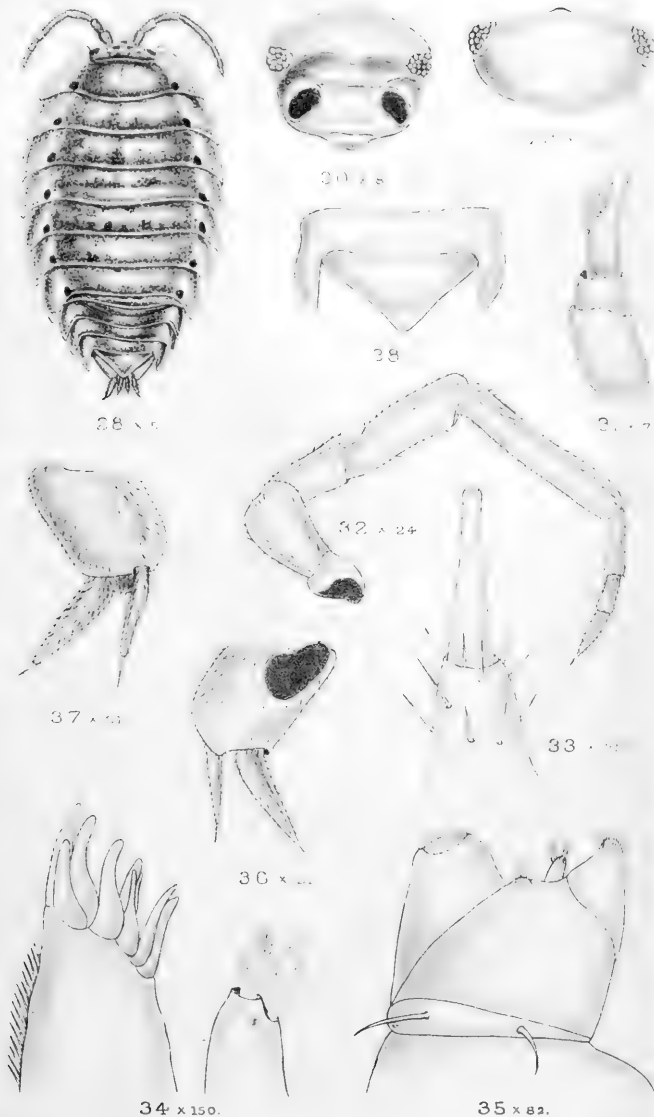
EMB. nat. nat.

LIGIA NATALENSIS sp.n. ♂♂ 9-18

LIGIA DILATATA Brandt ♂♂ 19-27

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H.C.K. del. ad nat.

ALLONISCUS MARINUS sp.n. figs 28-38.

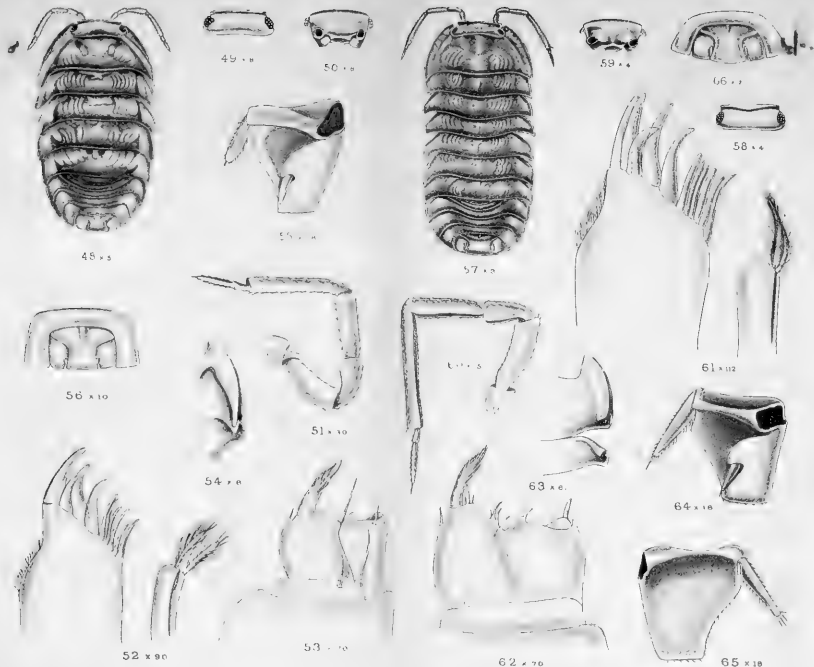


F.J.J. del. ad nat.

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PORCELLIONIDES PRUINOSUS (Bn), figs 39-47.





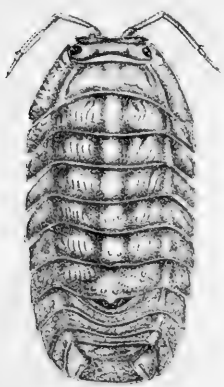
H. C. K. del. ad nat.

A. J. J. del. ad nat.

CUBARIS TRUNCATUS sp. n. figs 48-56.

CUBARIS AKERMANI sp. n. figs 57-66.

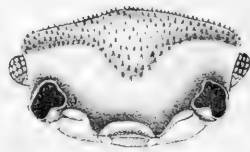
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67 x 14



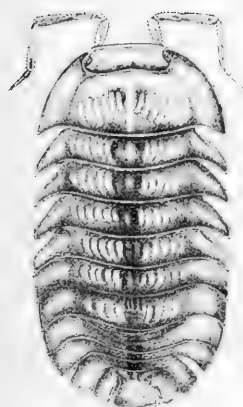
68 x 19



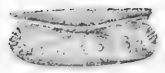
69 x 19



70 x 15



77 x 6



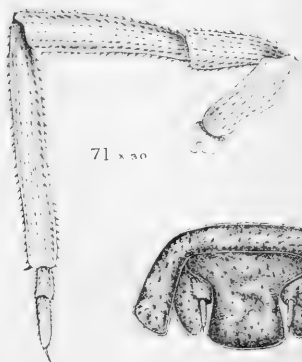
78 x 15



79 x 15



73 x 16



71 x 30



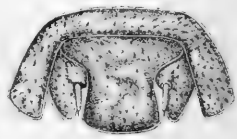
80 x 25



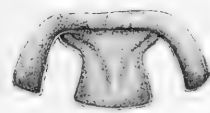
83 x 25



81 x 320



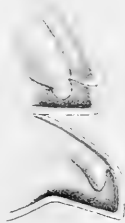
76 x 20



85 x 15



72 x 75.



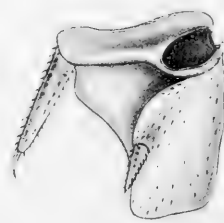
74 x 16.



75 x 50.



82 x 15.



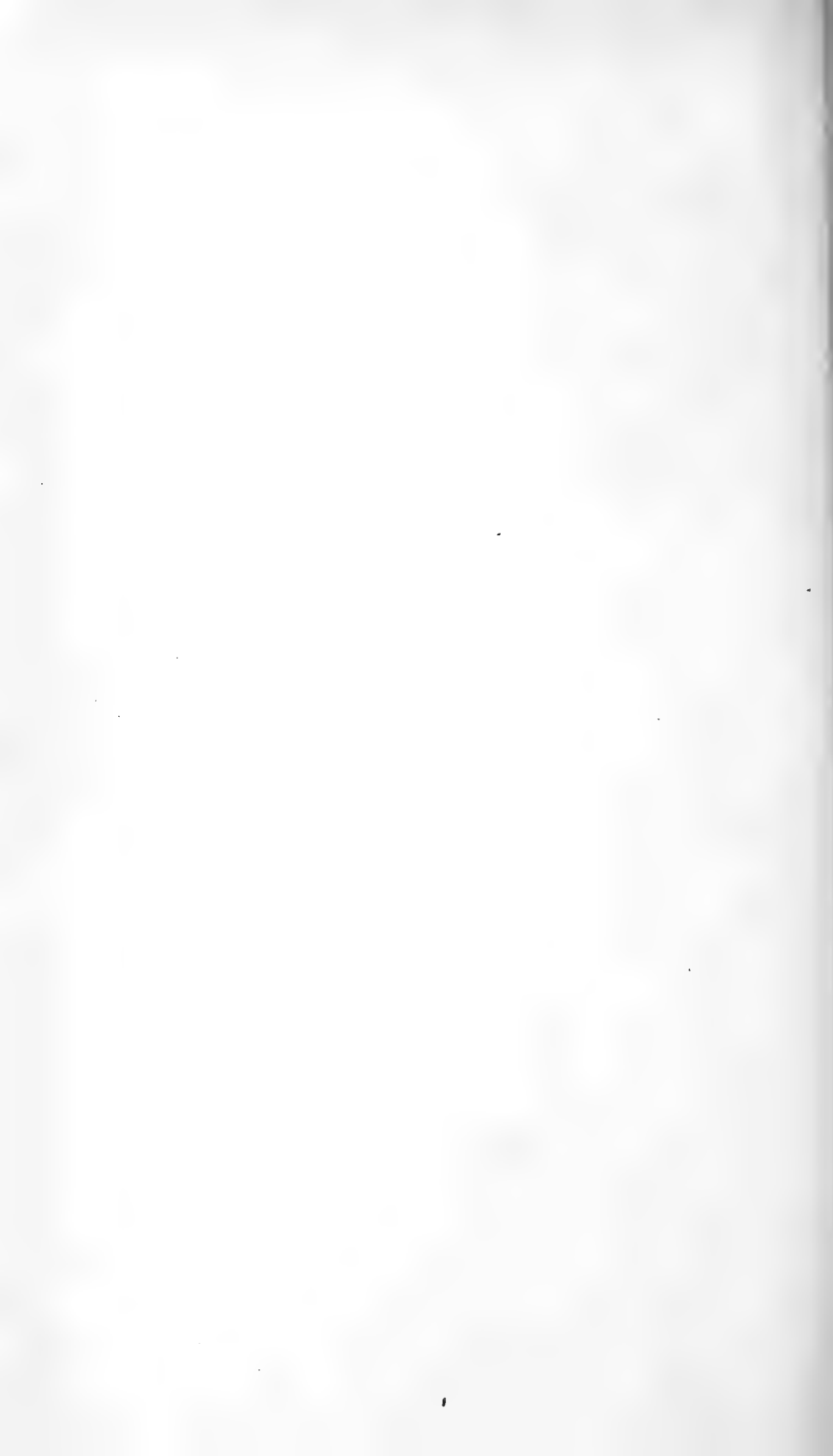
84 x 50

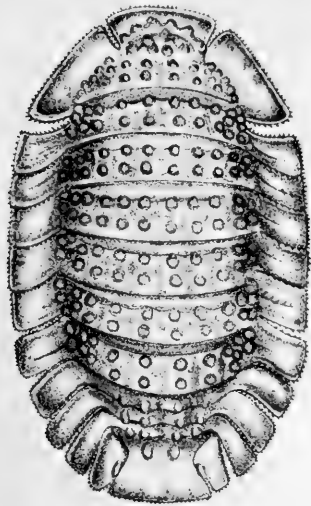
ERB.del ad nat.

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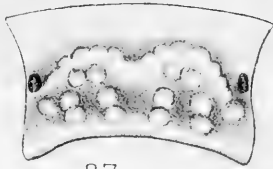
CUBARIS BARNARDI sp.n. figs 67-76.

CUBARIS GRISEUS sp.n. figs 77-85.





86 x 9.



87 x 15



93



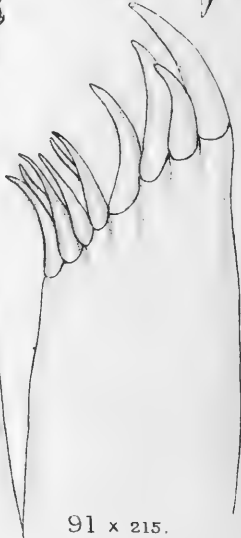
88 x 15.



95 x 50.



90 x 320.



91 x 215.



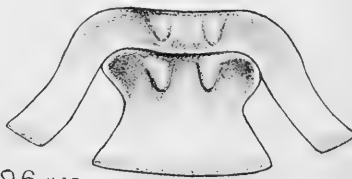
89 x 7.5.



94 x 50.



92 x 50.

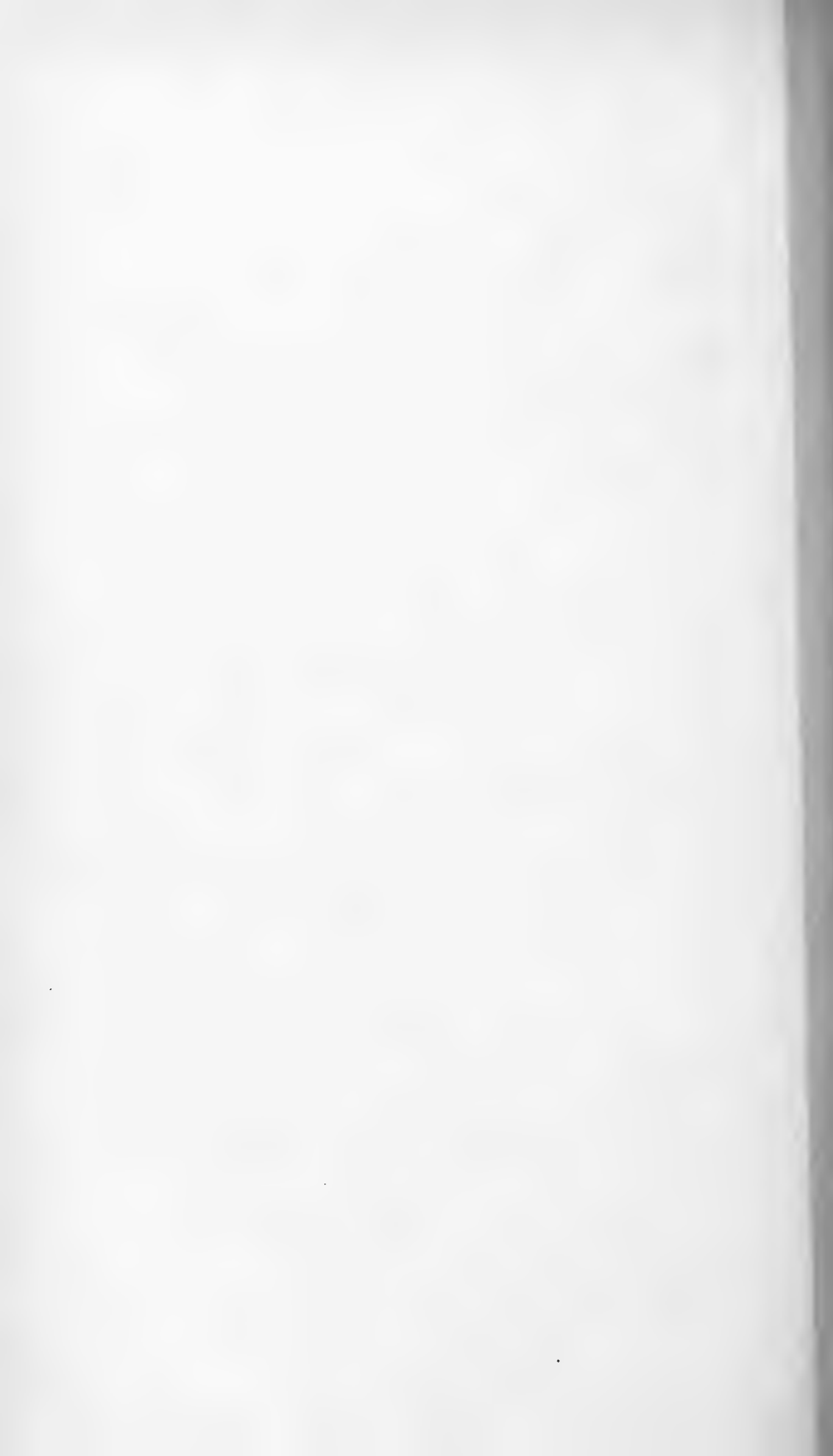


96 x 15

E.R.B. del. ad nat.

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ANCHICUBARIS FONGOSIENSIS gen. et sp. nov.



Four New African Gall Midges

By

E. P. Felt,

State Entomologist, Albany, New York.

THE gall-midge fauna of Africa, like that of many other groups, is exceedingly interesting and peculiar. A study of the world distribution of gall midges¹ shows that a number of the more widely distributed genera are found in Africa, and the presumption is that the list of these forms would be greatly increased if the fauna were better known. There are something like three hundred genera and presumably three thousand species of these fragile insects, and it is safe to state that only a very small proportion of the rich African fauna has come to the attention of entomologists.

The following new species, including representatives of two new genera, have been submitted for study through the courtesy of Prof. C. P. Alexander, of the State Natural History Survey, Urbana, Ill., U.S.A.

XENHORMOMYIA n. g.

The structure of this remarkable fly suggests a relationship to *Hormomyia* *H. Lw.*, and further study may show it to be a connecting link between the *Asphondylariæ* and the *Itonididinariæ*. It also exhibits characters in common with the American *Caryomyia* *Felt*—a genus which upon further study we have placed in the *Asphondylariæ*.

Xenhormomyia is readily distinguished from its allies by the distinctly constricted flagellate antennal segments

¹ 'National Academy of Science Proc.,' vol. iii, pp. 349-354.

of the male, the numerous low, looped circumfila and the presumably narrowly oval lobes of the ovipositor. Type *X. africana n. sp.*

Xenhormomyia africana n. sp.

The specimen described below was labelled "C. Akerman, Maritzburg, 1916." The type is deposited in the Natal Museum at Pietermaritzburg, Natal, South Africa.

MALE.—Length 6.5 mm. Antennæ dark reddish-brown, probably distinctly longer than the body, and with at least 10 and probably 14 segments, the 1st obconic, the 2nd disc-shaped, the 3rd and 4th free, the flagellate binodose, the 5th with a distinct constriction near the basal third and a slightly developed distal stem. The basal enlargement broadly oval, with a length nearly $\frac{1}{2}$ greater than its diameter, and with a series of about 10 low, looped circumfila, the distal enlargement with a length about twice its diameter, and with a series of 12 or more low, looped circumfila, both thickly clothed with short scale-like hairs as in *Asphondylia*. The 10th segment with both the basal and distal constrictions with a length approximately equal to their diameters, the terminal segment wanting. Palpi, the 1st segment and 2nd segment short, indistinct in the preparation, the 3rd with a length 5 times its diameter, and the 4th a little longer than the 3rd. Mesonotum dark reddish-brown, somewhat darker laterally. Scutellum dark reddish-brown. Postscutellum yellowish. Abdomen dark brown, rather thickly haired, wings hyaline, subcosta uniting with the somewhat heavily chitinated margin near the basal half. The nearly straight 3rd vein joining the margin at the apex of the wing, the 5th at the distal fourth, its branch at the basal third. Halteres yellowish basally, reddish apically, legs mostly a dark reddish-brown. Genitalia, basal clasp segment moderately long, stout, excavated mesially, terminal clasp segment rather short, stout, distinctly swollen near the middle and pectinate apically. Dorsal plate moderately long, broad, broadly and roundly emarginate,

the somewhat divergent lobes roundly triangular. Ventral plate rather long, deeply and roundly emarginate; the lobes rather long, stout, tapering. Type Cecid. 1808.

Xenhormomyia natalensis n. sp.

The large female described below was labelled "C. Akerman, Maritzburg." This insect may prove to be the female of *Xenhormomyia africana* described above, though it presents some distinct structural differences. The type is deposited in the Natal Museum, Pietermaritzburg, Natal, South Africa.

FEMALE.—Length 7 mm. Antennæ about as long as the body, sparsely haired, light brown, 14 segments, the 1st with a length about twice its diameter, the 2nd disc-like, the flagellate cylindrical, the 3rd and 4th free, the 5th with a length about 5 times its diameter, and with very irregular, low sinuous circumfila from near the base to the tip of the segment. Terminal segment cylindrical with a length about 5 times its diameter and apically a rudimentary, fusiform 15th segment with a length about $\frac{1}{3}$ the preceding. Palpi, 1st segment broadly oval, 2nd with a length about 3 times its diameter, the 3rd as long as the 2nd, more slender, the 4th $\frac{1}{2}$ longer than the 3rd, more slender and somewhat distorted near the middle. Mesonotum reddish-brown. Scutellum yellowish-brown, postscutellum a little darker. Abdomen dark reddish-brown, wings hyaline; costa reddish-brown, heavily chitinated basally, and near the basal fifth of the wing there is on its posterior margin a curved spur-like chitinated process. Subcosta uniting with the margin at the basal third, the 3rd vein apparently arising from the distal 4th of subcosta joins the margin at the apex of the wing; the 5th at the distal fourth, its branch at the distal third. Halteres yellowish basally, reddish-brown apically, coxæ and legs mostly reddish-brown, the tarsi somewhat darker, claws long, stout, strongly curved, simple, the pulvilli as long as the claws. Ovipositor short,

stout, the lobes at the dorsal angles narrowly oval, concave mesially, sparsely setose, and with the broadly-rounded tips nearly approximate. Type Cecid. 1807.

HETEROBREMIA n. g.

The peculiar type placed here is easily distinguished from *Homobremia* by the two widely separated linear processes extending from the posterior lateral angles of the ventral plate and reaching to the tip of the style. The genitalia are very complex, and there are also marked structural peculiarities in the antennæ. Type *H. furcata* n. sp.

Heterobremia furcata n. sp.

The peculiar midge described below was labelled "Lonji, Cameroon, West Africa, near the Ulou River." This locality is about fifty miles north of Kribi. The midges were recorded as resting in great numbers on spider webs in the trunk of a hollow tree, and were associated with *Homobremia agilis* described below. The type is deposited in the New York State Museum, Albany, N.Y., U.S.A.

MALE.—Length 1.5 mm. Antennæ $\frac{1}{2}$ longer than the body, thickly haired, dark brown, 14 segments, the 3rd and 4th fused, the 5th with stems as long and $2\frac{1}{2}$ times their diameters respectively. Basal enlargement subglobose, with a sparse basal whorl of long, stout setæ and a subapical circumfilum, one bow being greatly produced, the distal enlargement with a length about $\frac{1}{4}$ greater than its diameter, a subbasal, low circumfilum peculiar on account of its distinctly oblique course around the segment, a thick whorl of moderately long, strongly curved setæ near the middle, a subapical whorl of long, stout setæ, an apical and well-developed circumfilum, the latter with at least one greatly produced bow. Terminal segment, basal portion of the stem with a length nearly 3 times its diameter, the distal enlargement with a length over twice its diameter, somewhat swollen apically, and with a slender, fusiform appendage,

the latter nearly as long as the entire segment. Palpi, 1st segment with a length 3 times its diameter, the 2nd as long as the 1st, the 3rd a little longer than the 2nd, and the 4th one-fourth longer than the 3rd, and somewhat dilated near the distal fourth. Mesonotum reddish-brown. Wings hyaline, subcosta joining the anterior margin near the basal half, the area between it and costa more or less distinctly chitinised, the 3rd vein uniting with the margin at the apex of the wing and the 5th at the distal fourth, its branch at the distal third. Halteres pale yellowish, legs mostly dark brown. Claws strongly curved, unindentate, the pulvilli rudimentary. Genitalia, basal clasp segment moderately long, stout, and with a well-developed triangular setose lobe at the basal third, terminal clasp segment moderately long, stout, swollen basally, dorsal plate relatively short, broad, deeply and triangularly emarginate, the lobes tapering to a narrowly rounded apex. Ventral plate moderately long, the basal portion broad, truncate mesially and with long, rather slender, somewhat irregular processes extending posteriorly from the lateral angles as far as the tip of the style, the latter moderately long, stout. Type Cecid. 1806 B.

FEMALE provisionally associated with *Homobremia agilis*, described below, may be the opposite sex of this species, since all were associated.

Homobremia agilis, *n. sp.*

This specimen was labelled "Lonji, Cameroon, West Africa, near the Ulou River, altitude about 1000 feet." This is a locality about fifty miles north of Kribi. The insects, several species, were recorded as resting in great numbers on spider-webs in the trunk of a hollow tree. The type is deposited in the New York State Museum, Albany, N.Y., U.S.A.

MALE.—Length 1.5 mm. Antennæ $\frac{1}{2}$ longer than the body, thickly haired, dark brown, 14 segments, the 5th with stems $1\frac{1}{4}$ and $2\frac{1}{2}$ times their diameters respectively. The basal enlargement subglose, the distal enlargement with a length

about $\frac{1}{4}$ greater than its diameter. Circumfila moderately heavy, the basal film of the distal enlargement somewhat broad, its position varying but slightly from transverse. Palpi, 1st segment with a length over twice its diameter, the 2nd a little longer, broader, the 3rd a little longer and more slender than the 2nd, the 4th longer than the 2nd and somewhat swollen at the distal 4th. Mesonotum reddish-brown, wings hyaline. Halteres pale yellowish, the legs mostly dark brown. Genitalia, basal clasp segment rather long, slender, with a distinct mesial extension at the basal third. Terminal clasp segment rather long, slender, swollen basally. Dorsal plate short, broad, narrowly and somewhat deeply incised, the lobes roundly truncate. Ventral plate long, tapering, triangularly emarginate apically. Style long, slender. Type Cecid. 1806 A.

FEMALE (Provisional association).—Length 2 mm. Antennæ nearly as long as the body, sparsely haired, dark brown, 14 segments, the 5th with a stem $\frac{1}{3}$ the length of the cylindric basal enlargement, which latter has a length $2\frac{1}{2}$ times its diameter. 14th segment cylindric with a length 3 times its diameter and apically a rudimentary, tapering process, nearly as long as the segment and with a globose enlargement sub-basally. Palpi, 1st segment narrowly oval, the 2nd nearly twice as long as the 1st, the 3rd a little longer, more slender, the 4th $\frac{1}{4}$ longer than the 3rd. Mesonotum dark reddish-brown. Scutellum and post-scutellum yellowish orange. Abdomen dark brown. Colours otherwise nearly as in the male.

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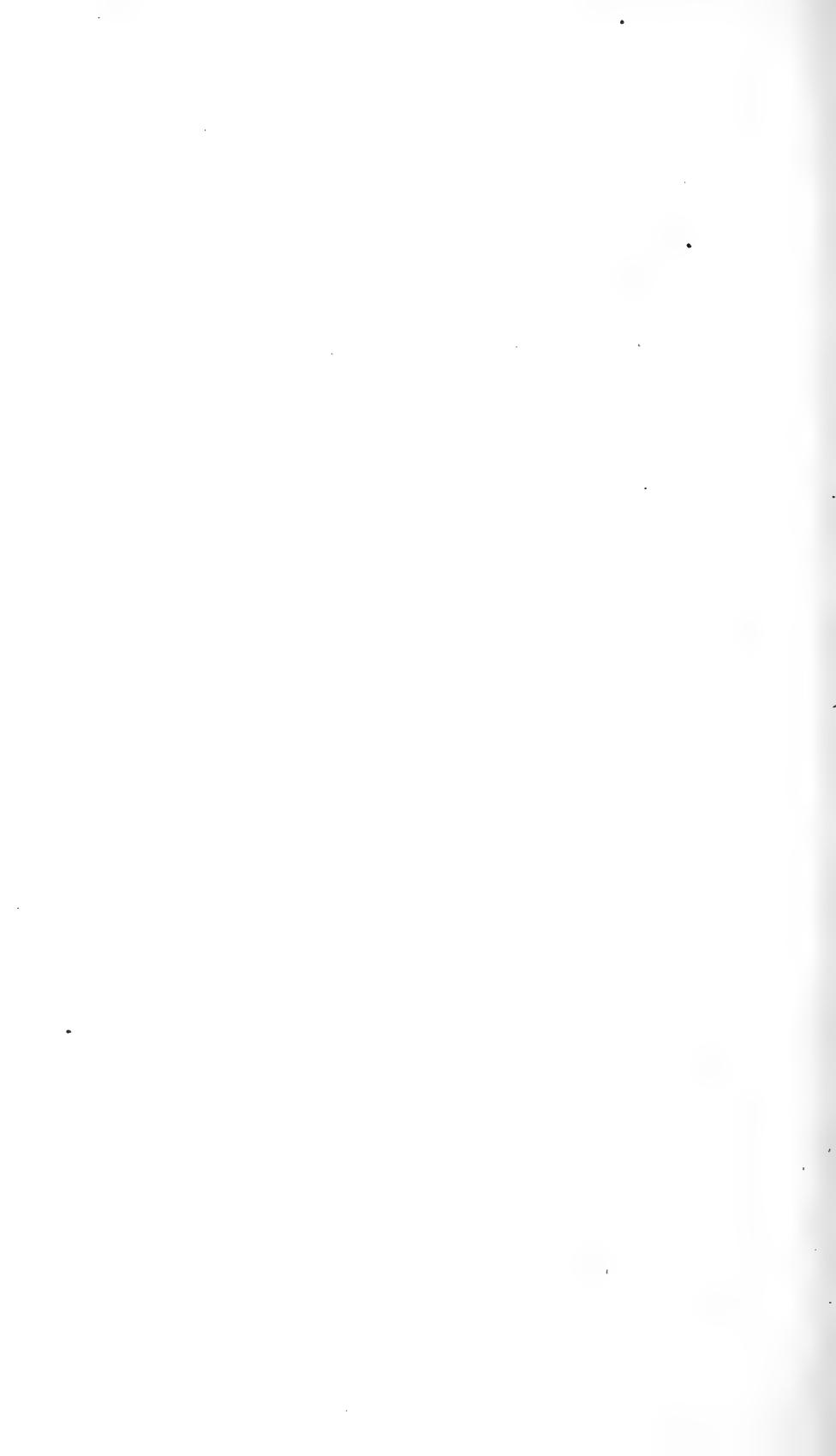
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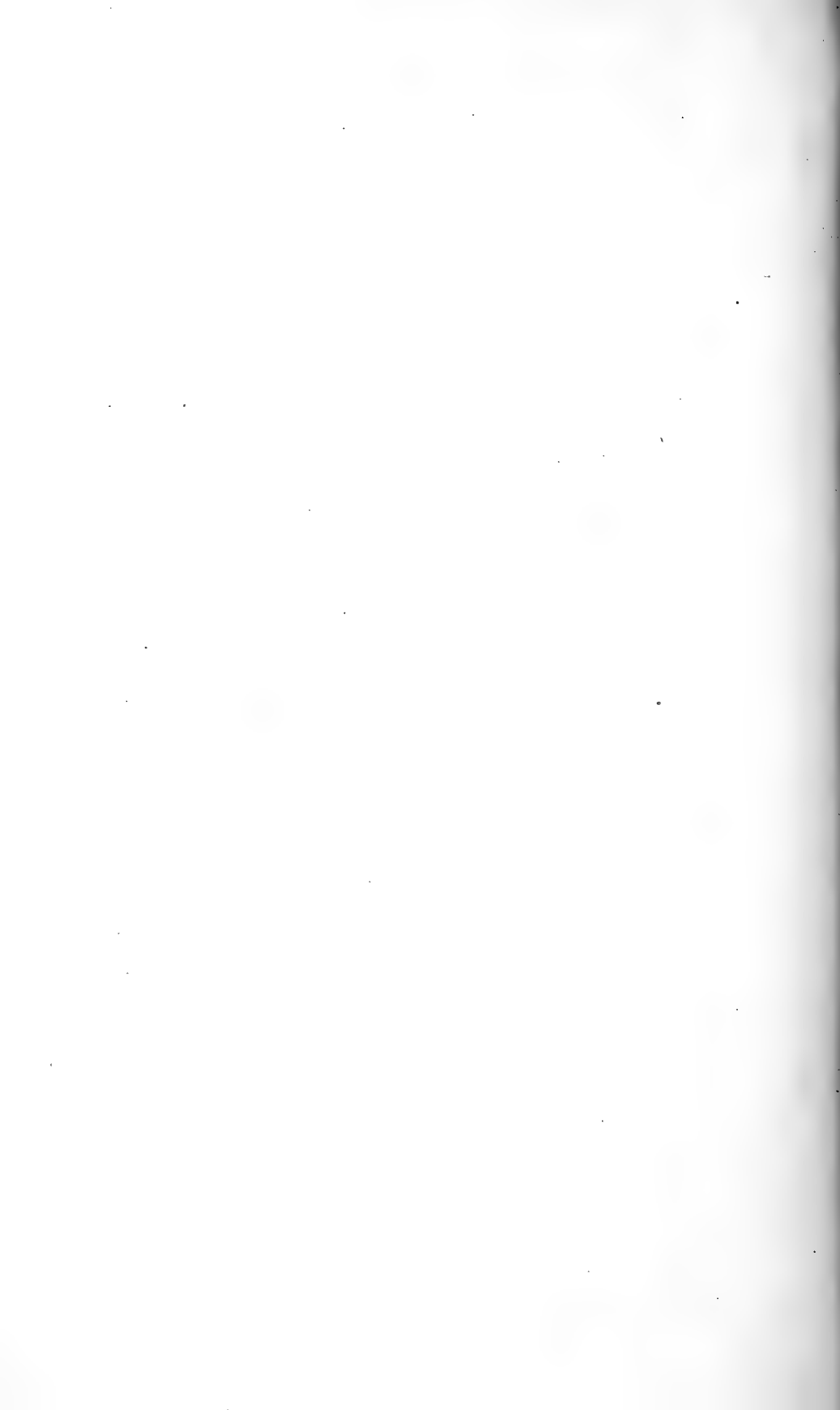
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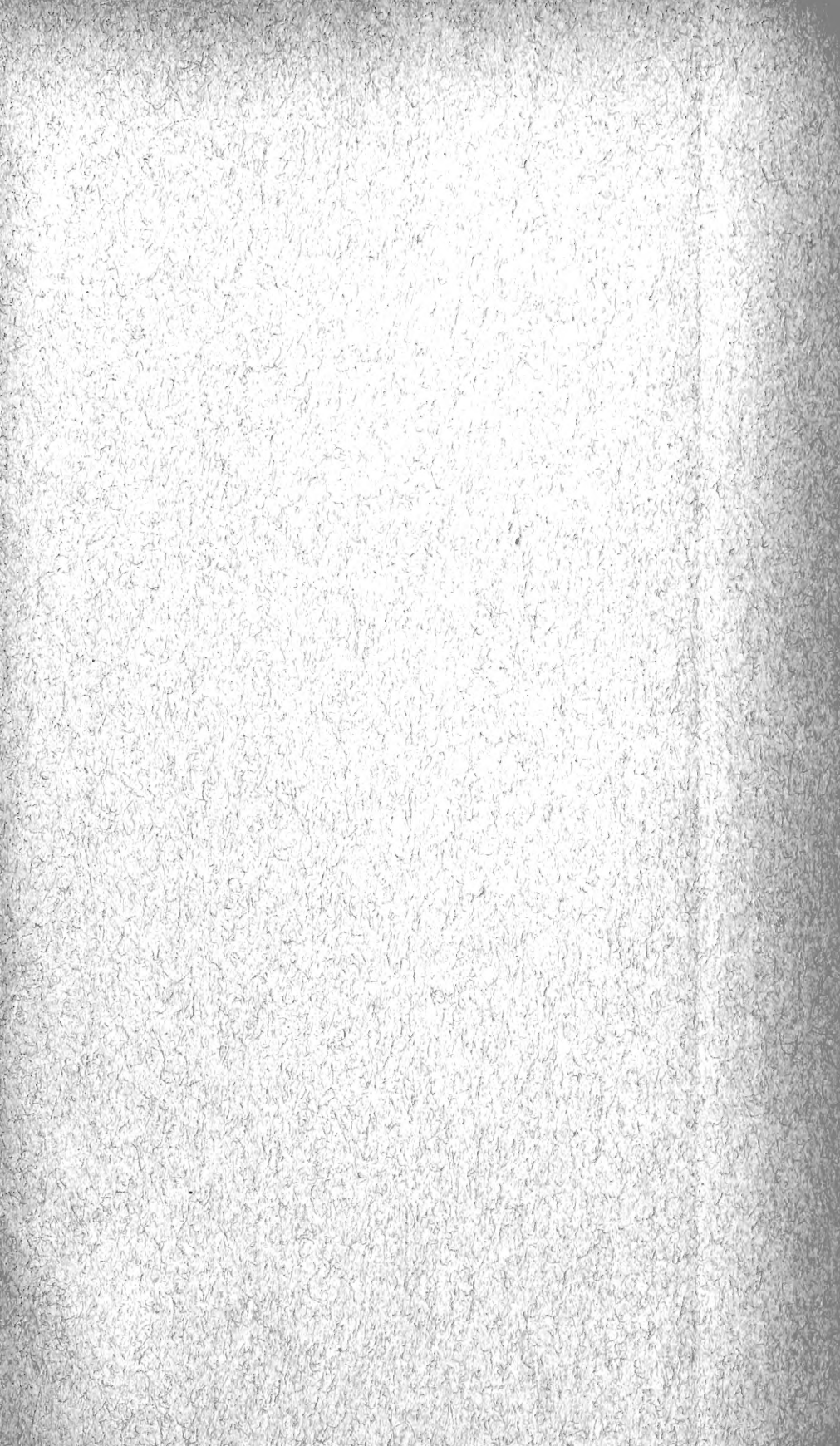
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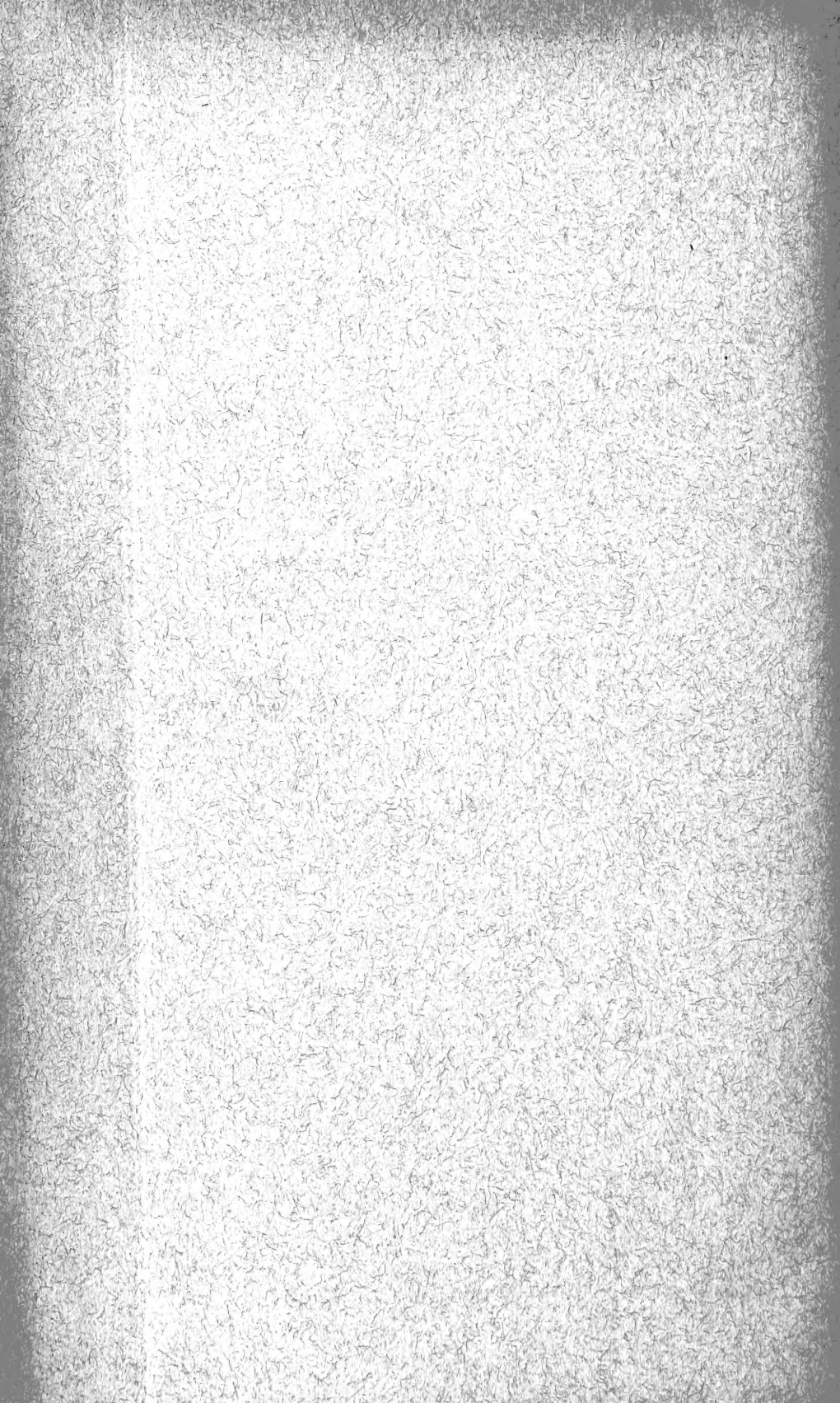
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